SPECIES AND SPECIATION IN PHYLOGENETIC SYSTEMATICS, WITH EXAMPLES FROM THE NORTH AMERICAN FISH FAUNA[1]

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Phylogenetic systematics as developed by Hennig (1950, 1966) is a system of methods and a view of the world designed to integrate systematics with the evolutionary "paradigm." By evolutionary "paradigm" we mean the world view that organisms always have parents and that organismic diversity is a byproduct of descent with modification. If our view of phylogenetic systematics is correct, or even partly so, the results derived from Hennig's methods should be of general utility to the evolutionary community. We shall attempt to show this utility by considering how the results of phylogenetic analysis can be used to infer the mode of speciation involved in the origin of species. Before doing so, however, we need to discuss what constitutes a species because our concepts will influence our choice of units to be analyzed.

SPECIES IN PHYLOGENETIC SYSTEMATICS

There is no consensus concerning either the nature of species-as-taxa or the importance of species among those who align themselves with Hennig's (1966) basic philosophy. This should come as no surprise because no consensus on either question has been reached by the rest of the biological community. At the risk of oversimplifying, we will define two basic attitudes. The first is what might be called the heuristic attitude. Rosen (1979: 277) defined species as "a population or group of populations defined by one or more apomorphous features, it is also the smallest natural aggregation of individuals with a specifiable geographic integrity that can be defined by any current set of analytical techniques." Nelson and Platnick (1981: 11) stated "species are simply the smallest detected samples of self-perpetuating organisms that have a unique set of characters." Rosen's statement is somewhat more restrictive, both in its inclusion of a geographic criterion and in its criterion that the species must have at least one apomorphous character. Both, of course, are not "process free" concepts since one (Rosen's) contains a statement based on character evolution while the other (Nelson and Platnick's) contains a statement based on reproduction. Nevertheless, both concepts are as heuristic as the authors can make them.

The second attitude might be termed the "process" attitude. The concept applied is not restricted to purely heuristic considerations but also the evolutionary nature of the entities. Of all phylogeneticists, Hennig (1966) himself was the most radical proponent of this attitude, a fact that is not always appreciated. Hennig (1966) spent a substantial part of his book arguing against heuristic concepts because he rejected ideal morphology and the "morphological system." To Hennig (1966: 79–80), it was phylogeny that was important, morphology being a way of getting at the phylogeny:

> The categories [= taxa] of phylogenetic systematics are not constructed by abstraction. They are not defined as bearers of a complex of characters that remains if, starting with the individuals, we subtract more and more characters that are specific to the individuals and then to progressively more inclusive groups of individuals. In the phylogenetic system the categories [= taxa] at all levels are determined by genetic [= genealogical] relations that exist among their subcategories [= taxa included within them]. Knowledge of these relations is a prerequisite for constructing these categories [= taxa], but the relations exist whether they are recognized or not. Consequently here the morphological characters have a completely different significance than in the logical and morphological systems. They are not themselves ingredients of the definition of the higher categories [= taxa] *but aids* used to apprehend the genetic [= genealogical] criteria that lie behind them. [Brackets and emphases ours.]

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Thus Hennig (1) rejected taxa as being defined by characters and (2) accepted that the only characters useful to the phylogenetic system were those that indicated genealogical connections. Hennig wished to work with entities having a "real" existence in nature. Of course one consequence of holding to this realist view of the world concerned species—to Hennig species are important only to the extent that they function in the evolutionary process. Thus a concept of a species as a unit functioning in the evolutionary process was an important tenet in his system. For all practical purposes, Hennig (1966) adopted the concept that species are (or were at some stage) reproductive units, but differed from such workers as Mayr (1963) and Simpson (1961) in rejecting chronospecies. However, he did more than this. Hennig understood very clearly that species have many of the characteristics of individuals, especially singular places of origin in time and space (1966: 81):

> If we now attempt to evaluate the categories [= taxa] of the phylogenetic system from the viewpoint thus gained, there can be no doubt that all the supra-individual categories [= taxa], from the species to the highest category rank, have individuality and reality. They are all (. . .) segments of the temporal stream of successive "interbreeding populations." As such they have a beginning and an end in time (N. Hartmann), and there is a constant causal connection between the phases in which they are found at different times (Ziehen). All this is missing in the categories [= taxa] of the morphological or typological system, which consequently are timeless abstractions (Woodger) and therefore have neither individuality nor reality.

It would be a mistake to assume that his condemnation was directed only at paraphyletic and polyphyletic taxa.

Hennig was perfectly aware that species and natural higher taxa (i.e., monophyletic taxa) were not the same sorts of individuals as individual organisms. Michael Ghiselin isn't the same sort of individual as *Homo sapiens,* who isn't the same type of individual as Vertebrata. Further, he recognized that the concept of individuality provided a link in our understanding of the transition between species, higher taxa, and natural hierarchies (see Hennig, 1966: 82–83). Specifically:

> Thus all categories [= taxa] of the phylogenetic system are characterized by individuality and reality, in contrast to the abstract and timeless categories [= taxa] of the morphological system. This does not mean that they are all "individuals" in exactly the same sense as the individual organisms that are the units of life, and which we ordinarily call individuals. Depending on the purpose we have in mind, we may emphasize the common traits in the mode of existence of the individuals (in the customary, strict sense) and the supra-individual systematic groups, or we may emphasize the differences. But, we cannot transfer uncritically all the criteria of individuality that characterize one category rank [= taxa at one rank] to other category ranks [= taxa at higher or lower rank] if we are to avoid faulty conclusions (Hennig, 1966: 83).

Hennig went on to emphasize that his thoughts, apparently developed from considering Hartmann (1942, not seen, cited in Hennig, 1966), applied only to taxa that were natural in the phylogenetic sense.

Michael Ghiselin (1969, 1974, 1980, 1981) independently came to the same conclusion as Hennig (1966): particular species are individuals and most emphatically, they are not mere clusters, nor are they natural kinds. This distinction is discussed at length by Ghiselin (1969, 1974, 1980, 1981) and by Hull (1976, 1983). Natural kinds are held by many philosophers to be eternal, immutable, and discrete. The problem, pointed out by both Ghiselin and Hull, is that philosophers have traditionally thought of particular species as natural kinds, even after accepting that evolution renders particular species as temporary and changeable entities. We stress the phrase "particular species" because there is an additional confusing aspect to the problem—"species" refers to both particular species such as *Homo sapiens* and *Pinus ponderosa* and to a natural kind that defines a class of entities on which process operates: although *Pinus ponderosa* is changeable and temporary, the natural kinds "biological species" and "evolutionary species" are eternal and immutable. There may be no individual species that are the natural kind "biological species," but that doesn't mean there has never been such a species or that such a species will never appear in the future. The possibility of biological or evolutionary species is a permanent possibility, entities which fill the class may evolve many times and in many places. An individual species, such as *Pinus ponderosa,* however, can evolve but once and once extinct is extinct forever.

PROCESS AND PATTERN IN SPECIATION

Speciation is one of the major processes underlying the patterns of descent that is the phylogeny of life on earth. As summarized by Wiley (1981) from many sources, speciation is not a single process but several more-or-less distinct processes that result in increases (and theoretical decreases) in the number of species in a clade. Patterns of genealogy at the level of species are the result of speciation. In some cases patterns of genealogy between clades are similar when examined in time and space. In other cases they are different. Different patterns may be the result of mistakes in reconstructing phylogenetic histories, the result of undetected extinctions or speciations, or the result of dispersals that alter the original pattern. These are all the result of our inabilities to detect what has actually happened. It is also possible that we have correctly reconstructed history and that the similarities and differences we observe in patterns of descent have a causal reason. Specifically, different modes of speciation might result in different patterns of genealogy in time and space. If so, and if we can couple differences of pattern with differences in mode, then we have additional tools with which we can gain a better understanding of the evolutionary process.

ASSUMPTIONS

Following the analysis of Wiley (1981) we shall explore the phylogenetic and biogeographic predictions derived from various proposed speciation modes that might be expected under certain conditions. The point of doing this exercise is to outline the conditions under which we can use genealogical and biogeographic information to determine which of the various modes might be operating. Obviously we do not expect all, or even most, groups to fulfill these conditions. At best we can hope that a few groups will fulfill the conditions and act as exemplars for studying the evolutionary process.

Assumption 1. Character evolution provides a reliable basis for inferring the history of speciation. There are two conditions under which this assumption would hold: (1) character evolution is coupled with speciation; or (2) character evolution keeps pace with lineage splitting, that is, there is enough anagenesis between lineage splits so that the sequence of splits leaves a "historical trail" that can be followed. Assumption 1 is violated if vicariance proceeds at a faster rate than character evolution, producing isolated populations that are similar. Subsequent evolution would not document the history of vicariance and a polytomy would result. (We shall see in a later section that a polytomy may exist even if character evolution does keep pace with vicariance.)

Two examples illustrate this. *Fundulus sciadicus* is composed of at least three disjunct populations (Fig. 1), presumably separated during the Kansan glaciation. If future divergent character change occurs before sympatry is achieved or before further splitting, a future phylogenetic reconstruction will not reflect the vicariance event involved. *Fundulus catenatus* is composed of at least five disjunct populations (Fig. 2), two of which might be correlated with the Ozark–Tennessee highlands vicariance event that we will discuss in a later section. Subsequent character evolution would not document the sequence of geographic isolation that this species has undergone.

Assumption 2. There are no extinctions of species in the clade. If we examine the results of particular speciation events, we must have some confidence that the species compared are the product of a single speciation event and not separated on the phylogenetic tree by several extinct, and unknown, species. If they are, then the differences observed may be the result of differences accumulated during several events. For example, *Fundulus parvipinnis* and *F. lima* are separated from other North American *Fundulus* by the Rocky Mountains and Great Basin. We know of fossil *Fundulus* from the Pliocene of California (Miller, 1945) and possibly from the Miocene of the Mohave Desert (Uyeno & Miller, 1963). Obviously ascribing the differences between Recent western *Fundulus* and their eastern counterparts to a single speciation event would be a dubious hypothesis. We simply don't know how many events were involved. The case of the *Fundulus nottii* species group (Wiley, 1977) is different. In this case (see Fig. 5 and discussion in a later section) there is no reason to believe that extinctions have occurred that would obscure the patterns because the group is distributed continuously over space.

Assumption 3. Dispersal has not obscured the original geographic pattern. Species pairs or clades that show large-scale dispersal may be identified

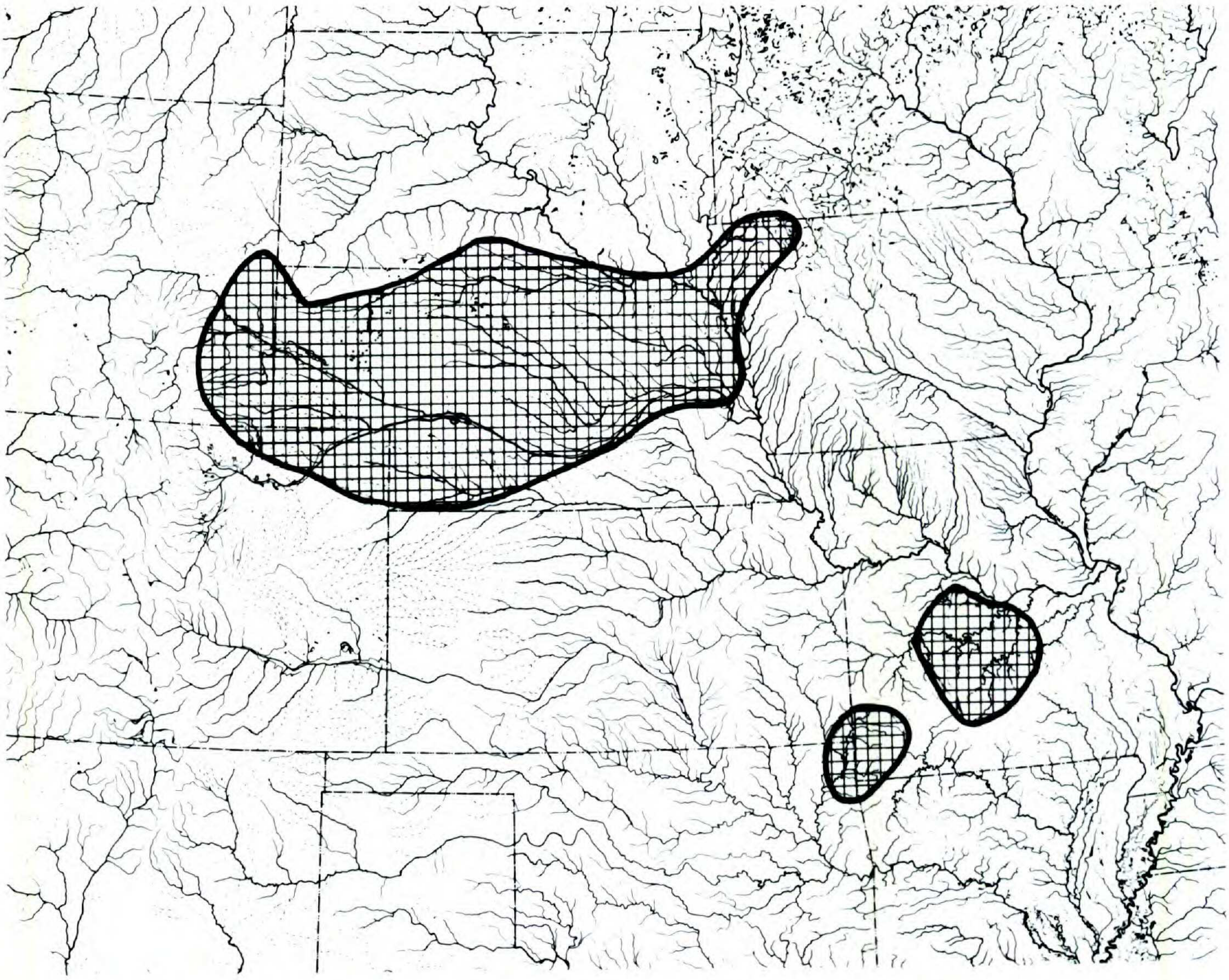

FIGURE 1. Distribution of *Fundulus sciadicus* (from Lee et al., 1980 and Ellis, 1914).

by widespread sympatry. For example, the pattern of speciation in the *Fundulus olivaceus* group (Fig. 3) is obscured by the widespread sympatry of *F. olivaceus* and *F. notatus* (Thomerson, 1966) and by the sympatry of *F. euryzonus* with both *F. notatus* and *F. olivaceus* (Suttkus & Cashner, 1981).

Obviously we cannot insure that any clade fulfills all three assumptions. However, we will suggest that some clades do because their histories and distributions show concordance with predictions based on particular modes of speciation and, in some cases, partial congruence in time and space with other groups. One final caveat—the modes we discuss are not our inventions and we have no interest in defending any of them as dominant or, in some cases, even realistic.

MODES AND PREDICTIONS

Following Mayr (1963), we may distinguish among three basic models of speciation. Reductive speciation involves lineage fusion; two species fuse to produce a third new species. While theoretically possible, there have been no documented cases of such events (Wiley, 1981). The nearest example would be a "compilospecies" (Harlan & deWet, 1963), in which one preexisting species simply absorbs the other. Additive speciation involves lineage splitting and reticulate speciation. The result is an increase in species diversity. There are several models for nonreticulate additive speciation that can be distinguished on the basis of the importance of geographic subdivision from essential (allopatric speciation) to nonessential (sympatric speciation). Additive speciation models are rich in predictions and we shall discuss several of them in sections below. The final model is "phyletic speciation," the proposition that there is species turnover within a single lineage without adding species in any one time frame. This "mode" has been rejected as a true mode of speciation by Hennig (1966) and by Wiley (1981) who pointed

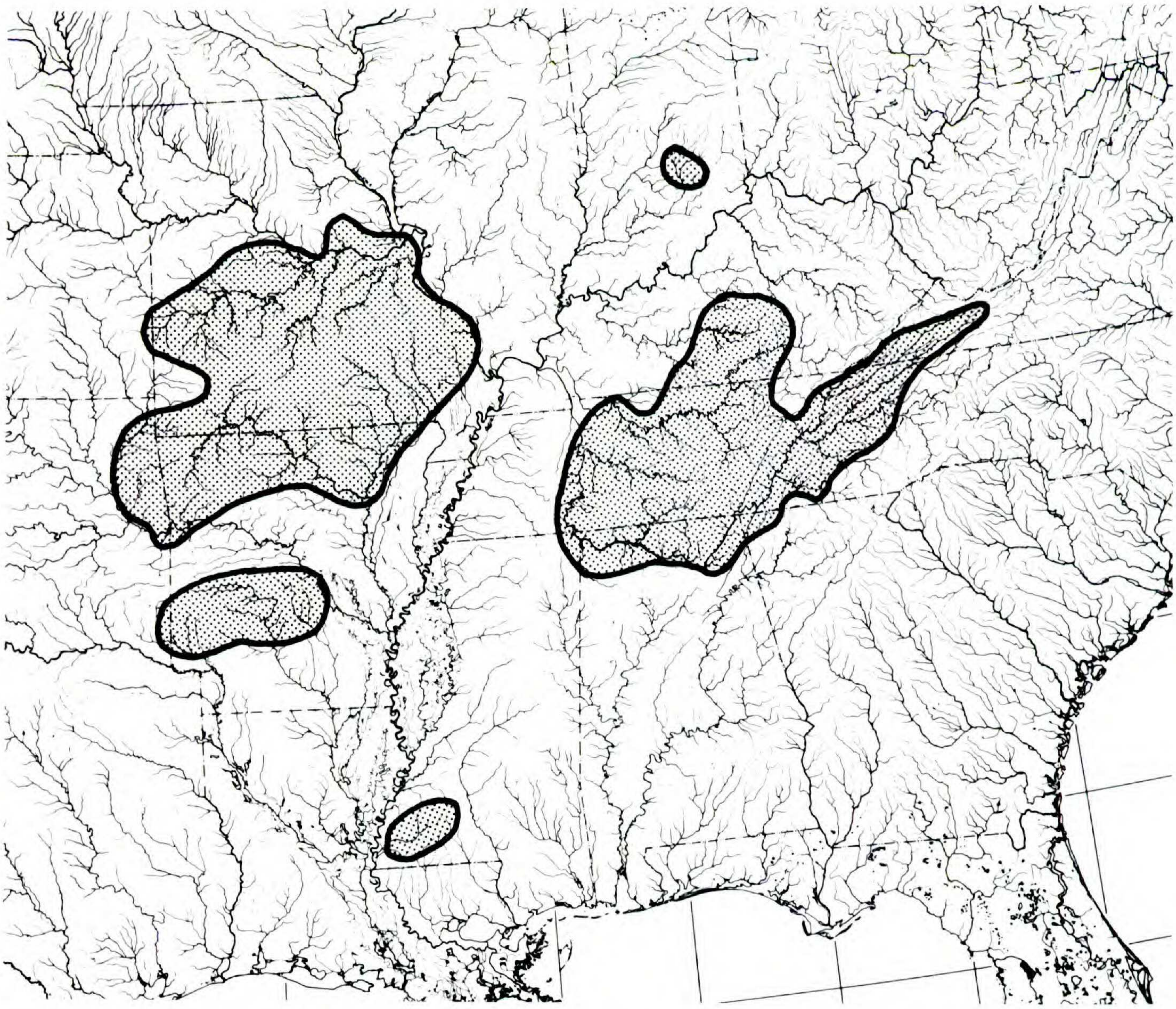

FIGURE 2. Distribution of *Fundulus catenatus* (from Lee et al., 1980).

out that subdividing a continuous lineage is an inherently arbitrary procedure. We shall not discuss it further.

ALLOPATRIC SPECIATION

Allopatric speciation is an umbrella term for a spectrum of modes that involve complete geographic separation of two or more subpopulations of a species during its evolution into two or more daughter species (one of which may be the ancestor itself). Allopatric speciation is thought to be the dominant mode by many investigators (cf. Mayr, 1963; Grant, 1971). Two basic models can be discerned based on population structure, a model that assumes gene flow is present and promotes lineage cohesion and one that assumes gene flow is absent or rare. The "gene flow model" can be further subdivided on the basis of the relative percent of the ancestral geographic range occupied by the subdivided populations. At one extreme we can envision equal partitioning of the ancestral range. At the other extreme we can envision the budding off of a very small part of the ancestral range, perhaps a single deme or even a single individual. Thus three models may be distinguished, two of which are extremes of a continuum.

ALLOPATRIC SPECIATION I—VICARIANCE

Vicariance speciation (Wiley, 1981) is a gene flow mode involving substantial geographic space. Differentiation may be manifested before geographic separation in the form of geographic variation, or it may not. Speciation may be rapid or slow depending on the amount of geographic variation existing before subdivision and the occurrence of evolutionary novelties after subdivision. Wiley (1981) suggested that the following phylogenetic and biogeographic predictions could be made based on this mode:

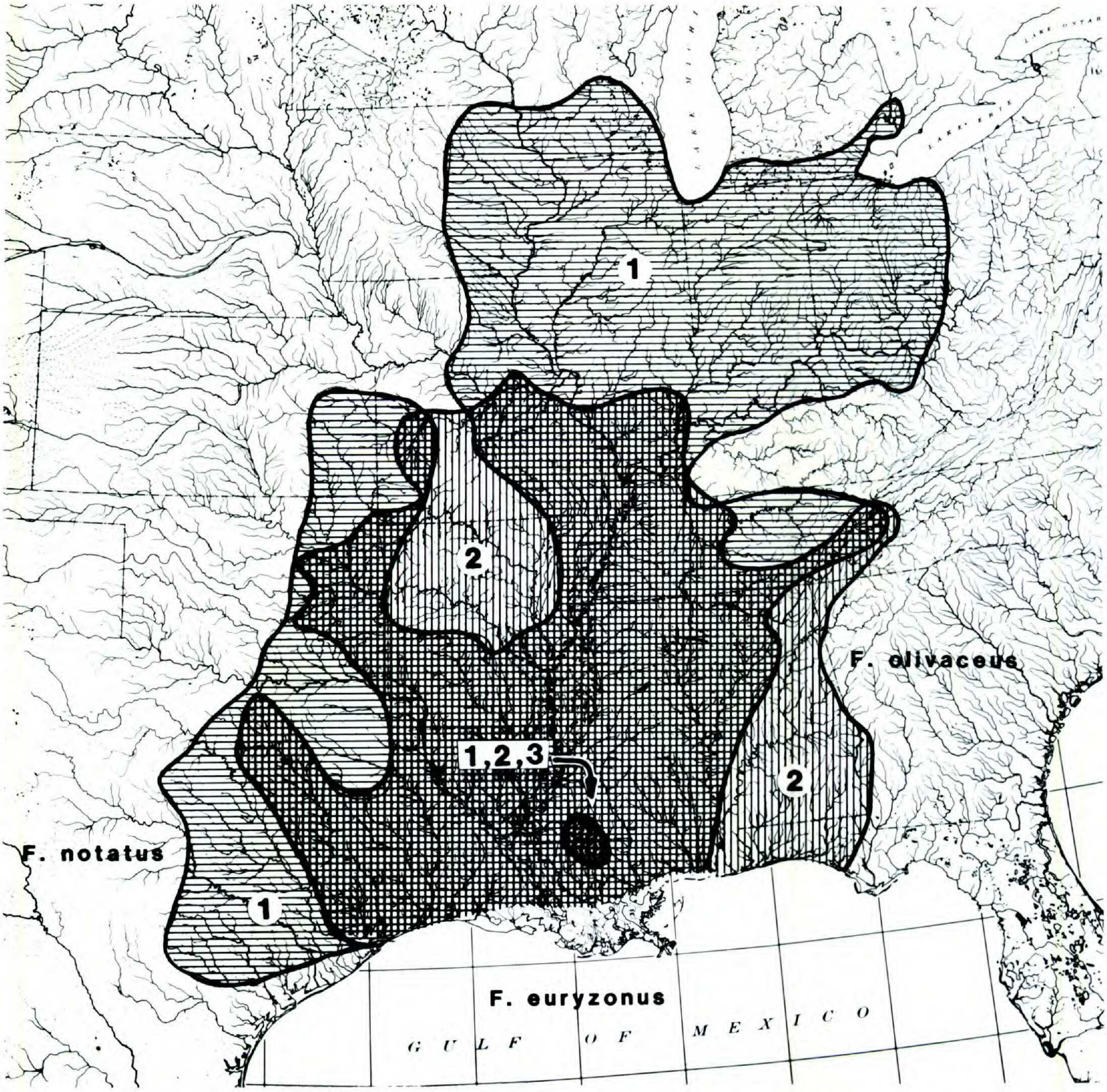

FIGURE 3. Distribution of the *Fundulus olivaceus* species group (from Lee et al., 1980 and Suttkus & Cashner, 1981).

1. Dichotomous phylogenies should predominate because of ancestral "extinctions," i.e., because there is no particular reason to think that either geographic subunit will be identical with the ancestor as a whole (Fig. 4).
2. The range of an ancestral species may be estimated by adding the ranges of daughter species.
3. Different clades should show common (congruent) patterns of speciation over time and space.

Predictions 1 and 3, dichotomy and some level of biogeographic congruence, are the important predictions. Of course, the congruence observed will be limited to those groups who (1) inhabit the same region, (2) are actually affected by the geographic event in question, and (3) have a history of character evolution that has kept pace with the subdivision.

Vicariance—Central Gulf Coast speciation. A number of clades of fishes contain sister species whose boundaries can be defined by the Mobile Bay drainage of the Central Gulf Coast of the U.S.A. Within the freshwater *Fundulus nottii* species group (Wiley, 1977; Fig. 5), *F. nottii* is found from streams draining into Lake Pontchartrain, Louisiana eastward to and including the lower reaches of the Mobile Bay drainage, Alabama. Its sister species, *F. escambiae,* is found from the Perdido River Drainage,

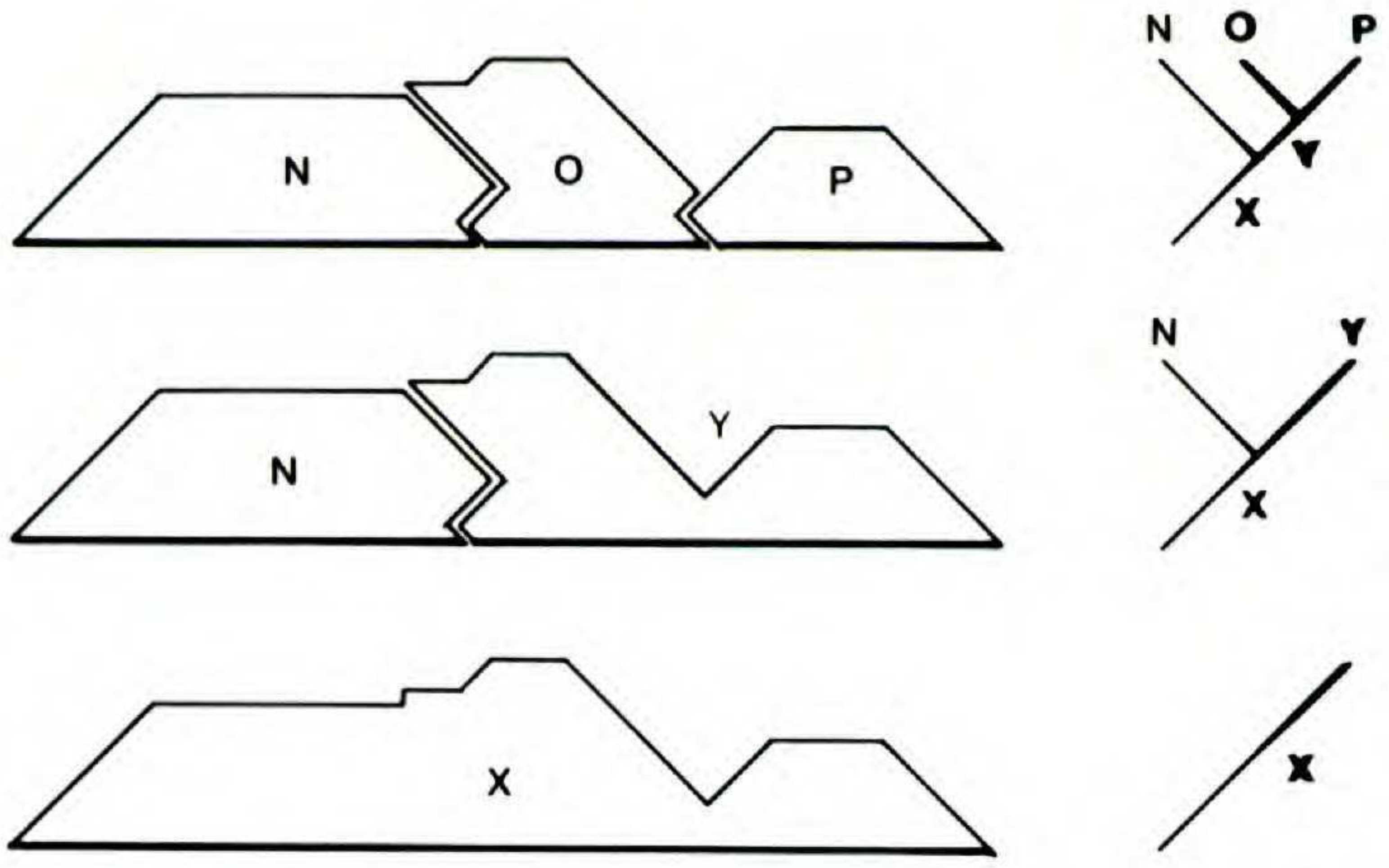

FIGURE 4. Speciation in the hypothetical clade NOP illustrating phylogenetic patterns expected in model 1 speciation.

Alabama to the lower Suwannee River, Florida. Phylogenetic analysis (Wiley, 1977) indicates that this species pair is most closely related to *F. lineolatus*, an Atlantic coastal species parapatric with *F. escambiae* (C. Gilbert, pers. comm.), and that the three together have affinities with the western sister pair *F. blairae–F. dispar* (see Fig. 5). There are several other fish groups showing a vicariant pattern at the Mobile Bay basin. These include:

1. *Fundulus confluentus* and *F. pulvereus* (Fig. 6), coastal and estuarine killifishes (Wiley, in press).
2. *Etheostoma chlorosomum* and *E. davisoni* (Fig. 7), freshwater darters (Howell, 1968; Page, 1983).

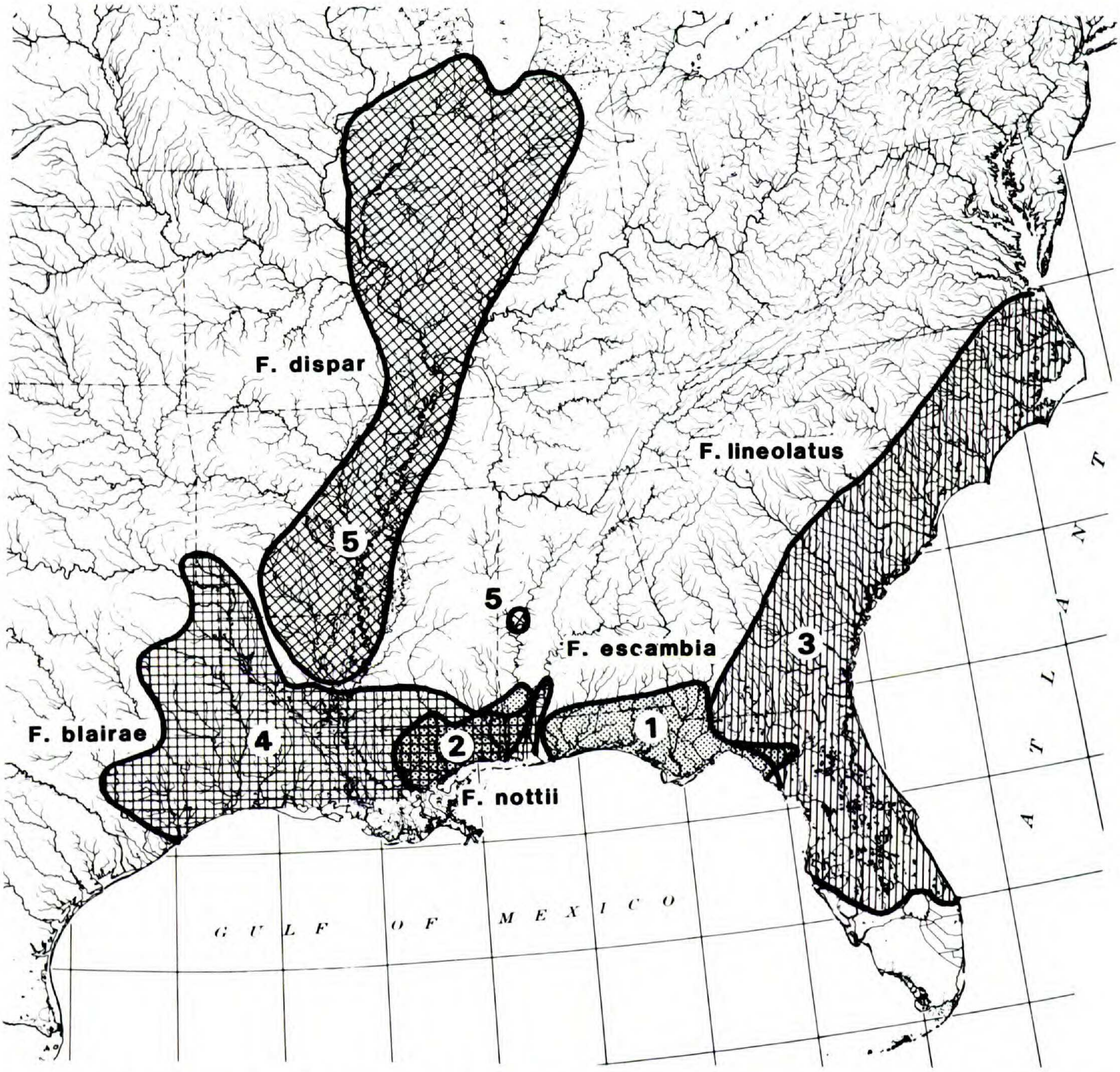

FIGURE 5. Distribution of the *Fundulus nottii* species group (from Wiley, 1977, with additional data from C. R. Gilbert, Univ. Florida). Tree: [4+5]+[3+(1+2)]. Characters supporting tree: see Wiley (1977, in press).

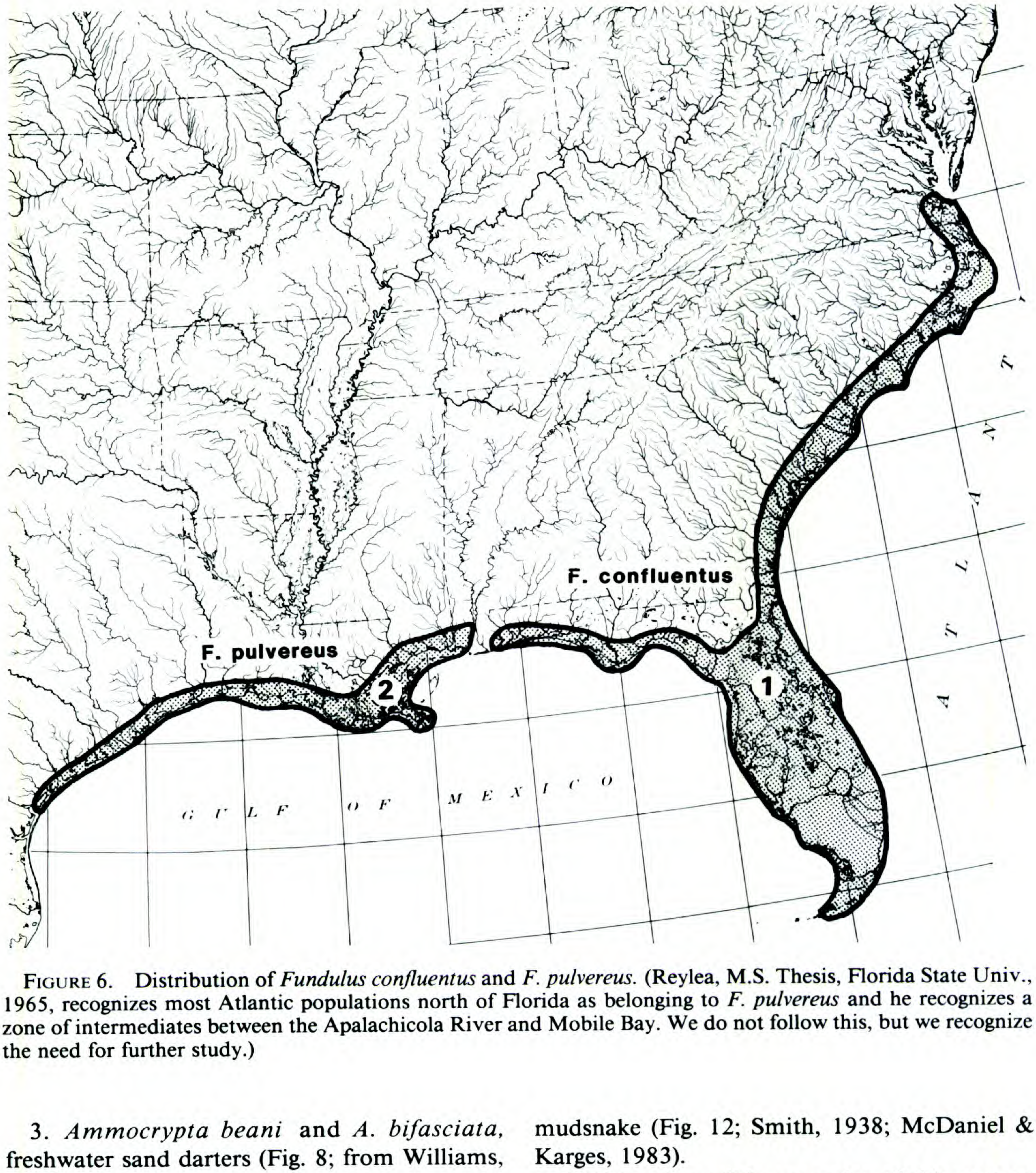

FIGURE 6. Distribution of *Fundulus confluentus* and *F. pulvereus.* (Reylea, M.S. Thesis, Florida State Univ., 1965, recognizes most Atlantic populations north of Florida as belonging to *F. pulvereus* and he recognizes a zone of intermediates between the Apalachicola River and Mobile Bay. We do not follow this, but we recognize the need for further study.)

3. *Ammocrypta beani* and *A. bifasciata,* freshwater sand darters (Fig. 8; from Williams, 1975).

4. *Hybopsis winchelli* and an undescribed species (Fig. 9), freshwater chubs (Clemmer, 1971; Lee et al., 1980).

In addition, several groups of snakes show vicariant patterns along the Mobile Bay basin, some on the level recognized as species, some as subspecies. These include:

1. *Nerodia rhombifera* and *N. taxispilota,* water snakes (Fig. 10; Mount, 1975).

2. Two subspecies of *Nerodia cyclopion* (Fig. 11; Mount, 1975).

3. Two subspecies of *Farencia abacura,* the mudsnake (Fig. 12; Smith, 1938; McDaniel & Karges, 1983).

Additional possible examples of this pattern also exist, but are complicated by the presence of a Mobile Bay drainage endemic, borders which do not exactly correspond to the event, dispersal, or the lack of an adequate phylogenetic hypothesis. These include:

1. *Notropis longirostris* and an undescribed species, two shiners, with the undescribed species endemic to the Mobile Bay drainage and *N. longirostris* found both east and west (Fig. 13; Swift, 1970; Lee et al., 1980; R. D. Suttkus, pers. comm.).

2. The *Notropis roseipinnis* species group,

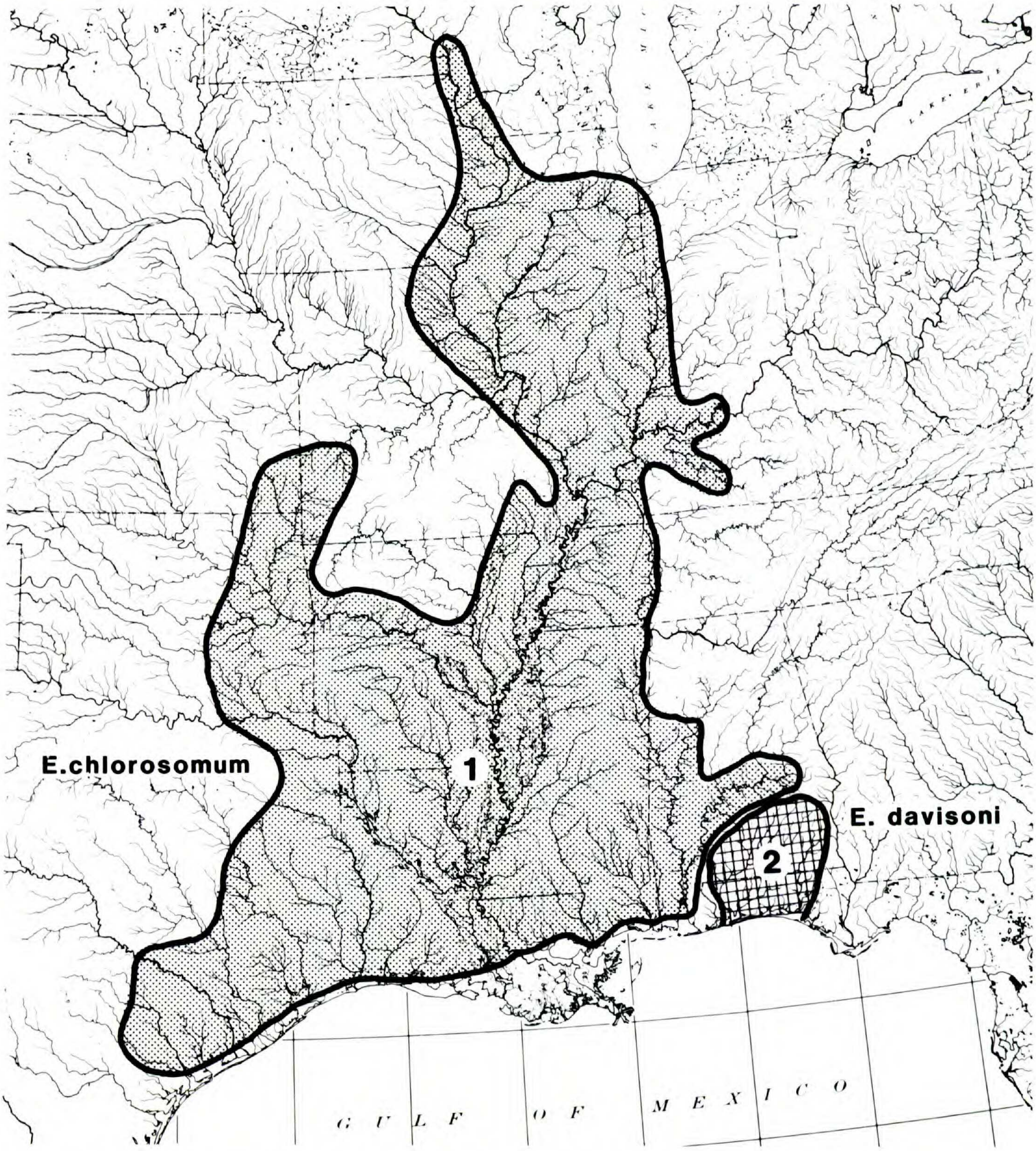

FIGURE 7. Distribution of *Etheostoma chlorosomum* and *E. davisoni* (from Page, 1983).

three shiners, with the Mobile endemic being the sister of the species *east* of the Mobile rather than west (Fig. 14). Snelson (1972) presented different possible phylogenies of these species and recently Stein et al. (1985) considered the above relationships to be most parsimonious.

3. *Ammocrypta meridiana,* a Mobile Bay endemic, is the sister species of the *A. vivax–A. pellucida* species group (Fig. 15; Williams, 1975; Page, 1981). This pattern is similar to that of the *Notropis roseipinnis* group and has a Mobile endemic, but differs from it and the *F. nottii* group in lacking a species east of the Mobile.

4. The *Notropis hypselopterus* species group in which there is an apparent peripheral isolate, *N. euryzonus,* closely related to the eastern species *N. hypselopterus.* The western species, *N. signipinnis,* shows a broad area of sympatry east of the Mobile (Fig. 16; Bailey & Suttkus, 1952; Suttkus, 1955; Gilbert & Platania, 1980).

5. *Percina sciera* and *P. nigrofasciata* (Fig. 17) show a pattern opposite of the *Notropis hypselopterus* group with the eastern species being widely sympatric with its sister *west* of the Mobile. This is further complicated by having two additional species (*P. aurolineata* and *P. lenticula*) of this clade in the middle of the distributional pattern of the clade (Lee et al., 1980; Page, 1981).

6. Two species of the turtle genus *Sternotherus*, *S. carinatus* and *S. minor*, show a pattern that might have resulted from a vicariance event involving the Mobile Bay drainage, but the pattern is complicated by the presence of *S. minor* in the Pearl River drainage of Mississippi and Louisiana (Fig. 18; Tinkle, 1958).

7. Two subspecies of the cottonmouth, *Agkistrodon piscivorus* (Fig. 19; Conant, 1975), two races of kingsnakes, *Lampropeltis getulus*, and two races of the pinesnake, *Pituophis melanoleucas*, have borders that correspond to a Mobile Bay vicariance (Mount, 1975) but in each case there are additional races or subspecies and there are no phylogenetic hypotheses demonstrating that the races with borders at the Mobile Bay drainage are closest relatives.

Another group of species show evidence of a more western vicariance event loosely associated with the Mississippi River. Within the *Fundulus nottii* species group, *F. blairae* and *F. dispar* are largely confined to the western part of the range (Fig. 5) and are the sister group of the eastern members of the group. A similar pattern is seen in *Ammocrypta*, with *A. clara* being the sister species of the *beani–bifasciata* species pair (Fig. 8). Additional examples might include:

1. *Notropis sabinae*, the sister species of the *N. longirostris* complex (Swift, 1970; Coburn, 1982; Fig. 13).

2. *Notropis umbratilis–N. ardens* species pair, sister group of the *N. roseipinnis* group (Snelson, 1972; Mayden, unpubl. data; Fig. 14).

Other groups may show a similar pattern, but the phylogenetic relationships among the members have not been investigated. These include:

1. Two subspecies of the turtle *Deirochelys reticularia* (Fig. 20; Zug & Schwartz, 1971), but there is a third subspecies.

2. "*Notropis*" *amnis* and the *Hybopsis amblops* complex (Fig. 9), but there are at least five species inhabiting other regions whose relationships are not known (Clemmer, 1971; Coburn, 1982; Mayden, unpubl. data).

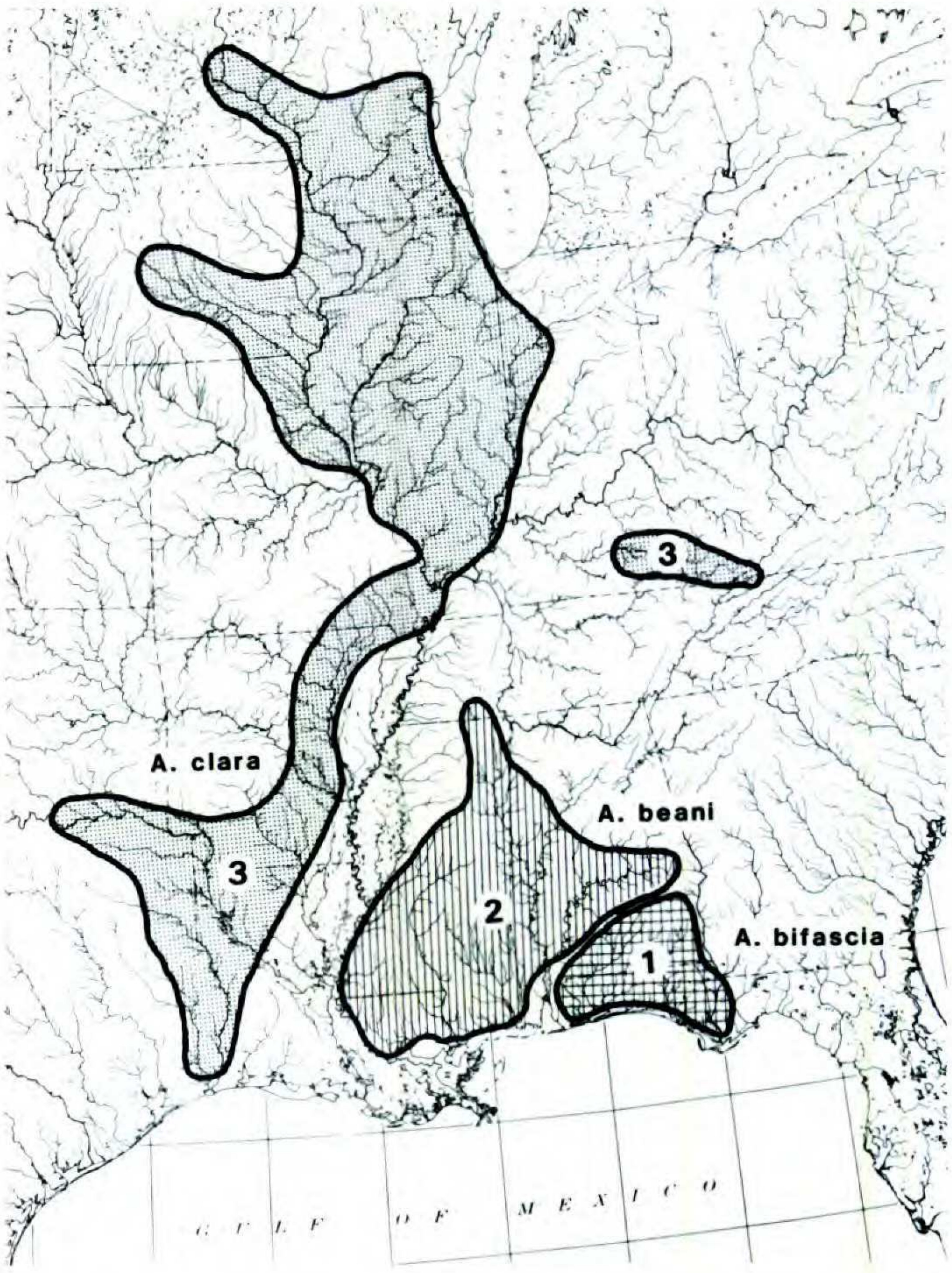

FIGURE 8. Distribution of the *Ammocrypta beani* species group (from Williams, 1975). Tree: 3+(1+2). Characters supporting tree: see Williams (1975).

In summary, there are possibly two large-scale vicariance events on the Northern Gulf Coast, one splitting the areas east and west of the Mobile Bay drainage and one involving the areas east and west of the Mississippi River. For those groups that show both patterns, it appears, based on the phylogenies, that the vicariance centering around the Mississippi is older than that centering around the Mobile Bay.

Vicariance—the Central Highlands. The Central Highlands of the U.S. may be broadly conceived of having two major components. The Interior Highlands comprises the Ozark Plateau and Ouachita Highlands. The "Tennessee Highlands" comprises the Interior Low Plateau, the Ridge and Valley Province, and the Blue Ridge Province—essentially that part of the Central Highlands drained by the Ohio, Tennessee, and Cumberland Rivers between the Appalachian Divide and the Coastal Plain. The faunas of interest are largely confined to high gradient streams, which usually have clear waters and rocky bottoms. Both areas have faunal (and no doubt floral) endemics and the closest relative(s) of an endemic in one area is likely to be found in the other area. In Figure 21, we have plotted

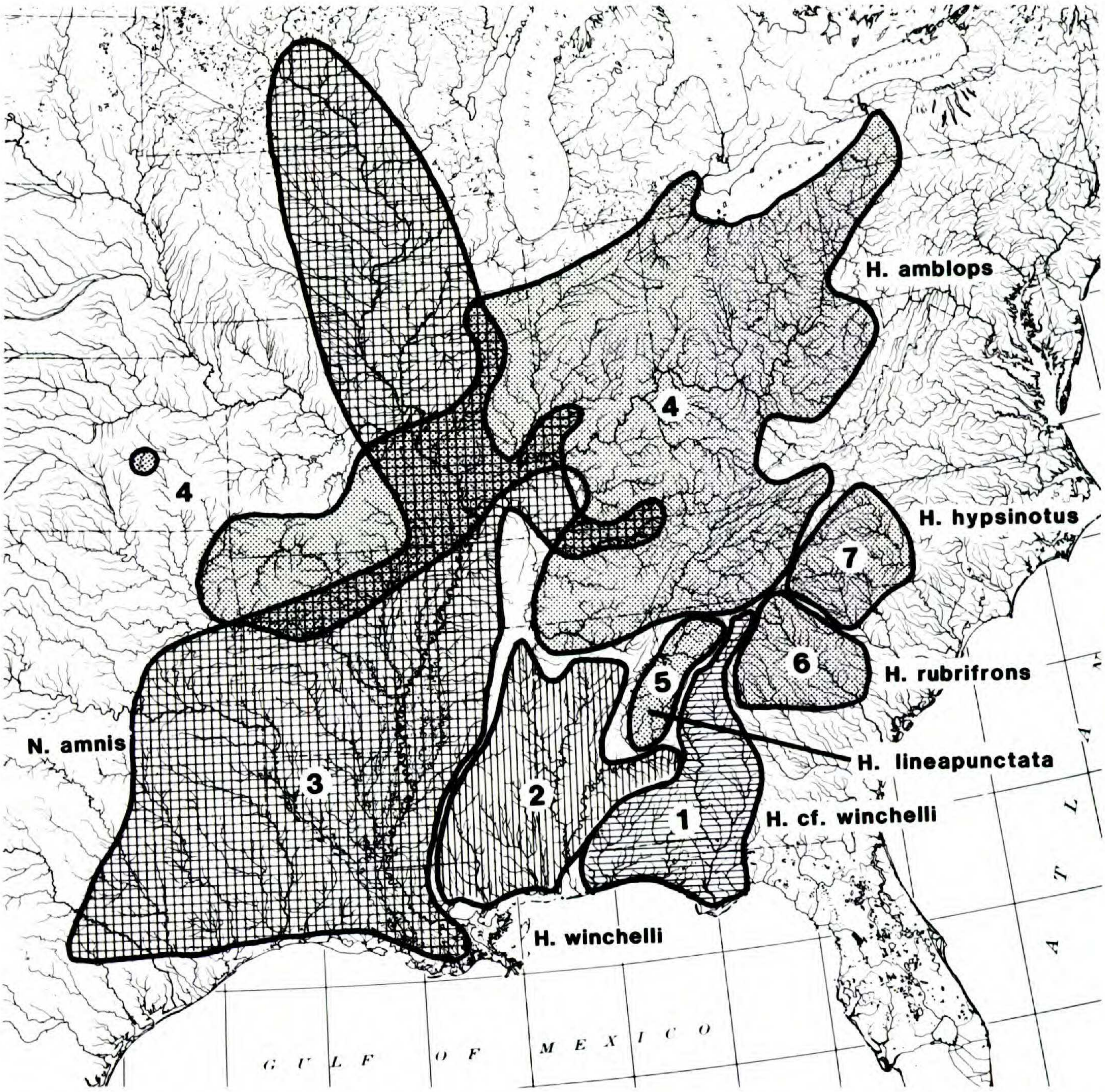

FIGURE 9. Distribution of *Hybopsis amblops* and related species (from Lee et al., 1980). Tree: (1+2)+3+4+5+6+7. Characters supporting the monophyly of the group: (1) oval orbit, (2) prominent lateral spines on the neck of the urohyal, (3) broad parasphenoid, (4) long neck on first basibranchial, (5) enlarged first pair of hypobranchials, and (6) elongate interhyal (Mayden, unpubl. data).

the total ranges of 44 species of freshwater fishes whose ranges are largely confined to one or both regions of the Central Highlands. (The many areas plotted north of these regions define various disjunct populations of species found in the region.) Not shown on this map, but plotted on subsequent maps are the ranges of close relatives outside the Highlands. Further, we do not show or discuss the large numbers of species endemic to various areas of the Tennessee or Ozark Highlands. The southern boundaries of the majority of the species shown in Figure 21 are largely congruent and form a border with the margins of the Cretaceous sea coincidental with the Coastal Plain. The northern boundaries of the Central Highlands fauna are not distinct owing to numerous disjunct populations of species otherwise confined to the two regions.

Geologic data indicate that prior to the Pleistocene many of the streams of Ohio, Indiana, and Illinois were high gradient and thus suitable for highland fishes (Thornbury, 1967; see Mayden, 1985, for summary). Further, drainage patterns were different, and what is now loosely referred to as the "Central Lowlands" was a highland region prior to the Pleistocene. Much of the

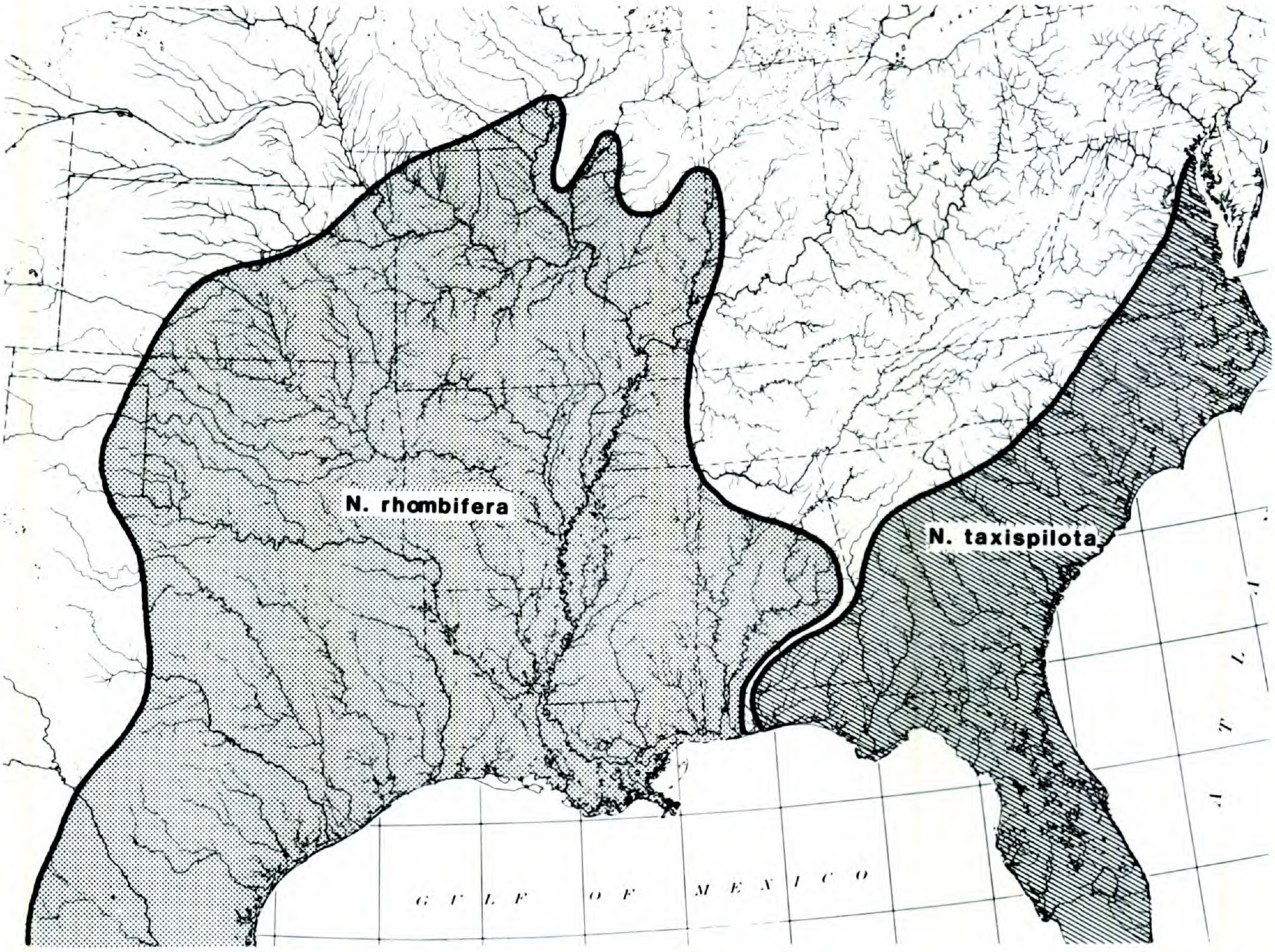

FIGURE 10. Distribution of *Nerodia rhombifera* and *N. taxispilota* (from Mount, 1975 and Conant, 1975).

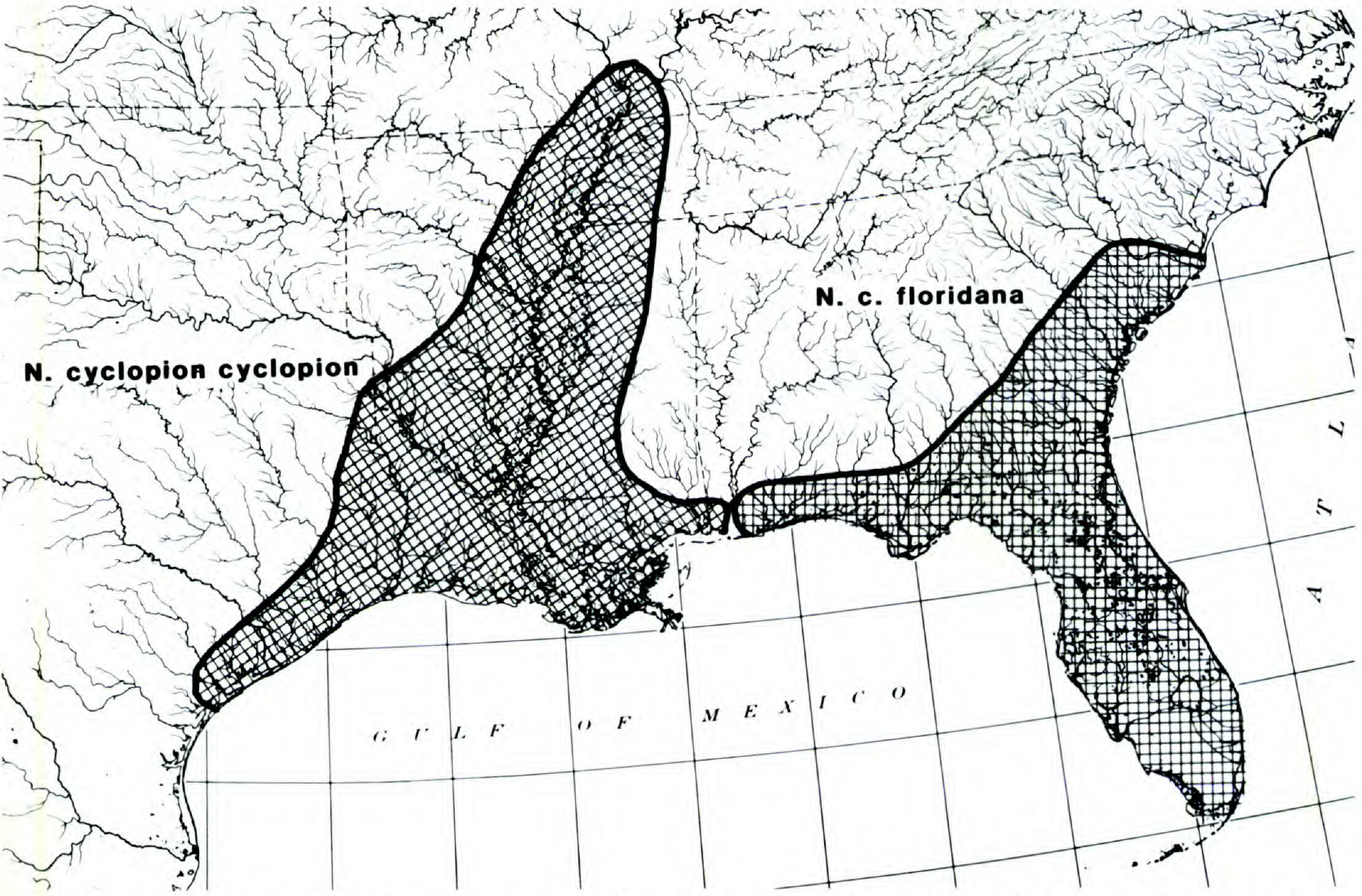

FIGURE 11. Distribution of two subspecies of *Nerodia cyclopion* (from Mount, 1975 and Conant, 1975).

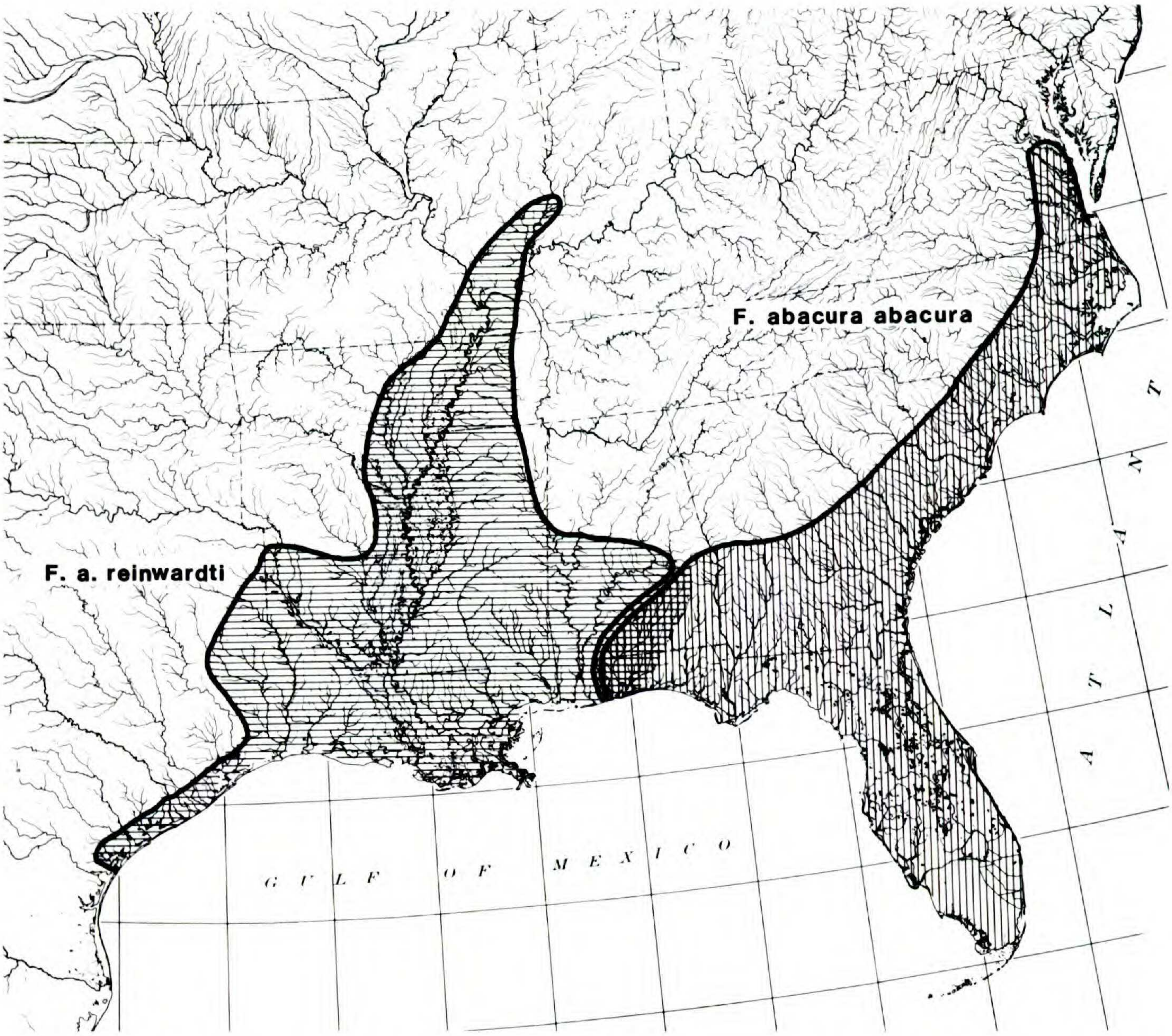

FIGURE 12. Distribution of two subspecies of *Farencia abacura* (from Smith, 1938 and McDaniel & Karges, 1983).

Tennessee Highlands was drained by the Teays River (labeled 9 in Fig. 22) that joined the Mississippi north of St. Louis. To the south the old Ohio (labeled 10 in Fig. 22) joined with the Cumberland to empty directly into the Mississippi and did not join with the Tennessee (see Hocutt et al., 1978, for a review). The present drainages are a consequence of Pleistocene phenomena. Thus, prior to the Pleistocene there is evidence that (1) the highland fauna covered a more extensive geographic area than today and (2) the drainage patterns were much different.

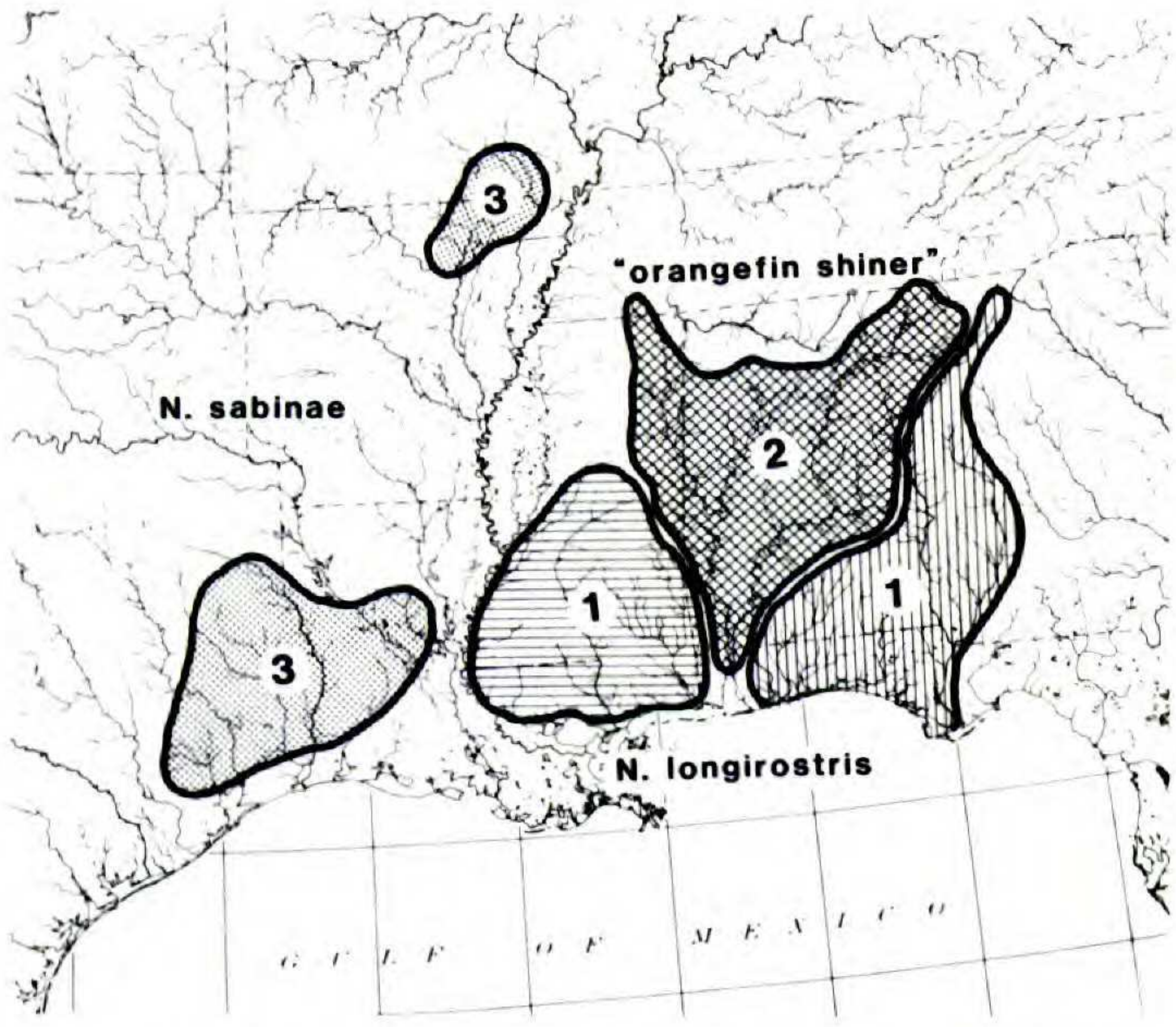

FIGURE 13. Distribution of the *Notropis longirostris* group (from Lee et al., 1980 and R. D. Suttkus, pers. comm.). Tree: 3+(1+2). Characters supporting monophyly of the group: (1) maxillary process of palatine elongate and anteriorly directed, and (2) enlarged plate-like second infraorbital (Mayden, unpubl. data). Characters uniting (1+2): see Swift (1970).

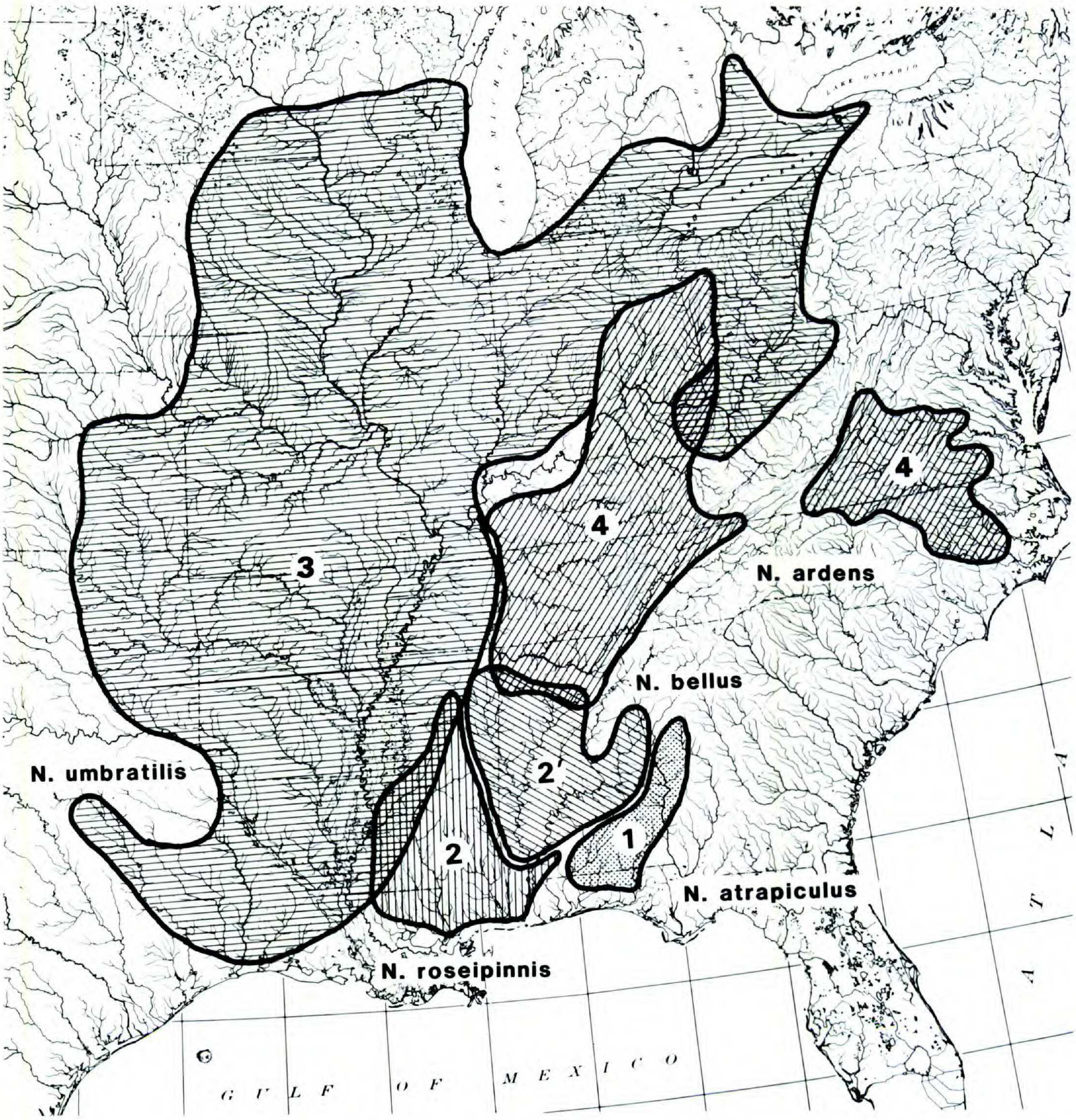

FIGURE 14. Distribution of the *Notropis roseipinnis* species group (from Lee et al., 1980). Tree: [3+4]+[2+(1+2′)]. Character uniting the group: breeding colors of males consisting of bright blues and reds (Mayden, unpubl. data). Character uniting (3+3): dark vertical bars on dorsum of breeding males (Mayden, unpubl. data). Relationships of [2+(1+2′)] are discussed in Stein et al. (1985).

The distinctiveness of the Central Highlands is partly reflected by the presence of species largely endemic to both areas. Among these are the minnows *Notropis galacturus* (Fig. 23) and *N. boops* (Fig. 24), the extinct sucker *Lagochila lacera* (Fig. 25), and cavefish *Typhlichthys subterraneus* (Fig. 26), the darter *Percina evides* (Fig. 27), and the salamander *Eurycea lucifuga* (Fig. 28). The distinctiveness of each region is also reflected by the presence of numerous endemic species that are not considered in this analysis.

When we presented data at the symposium concerning the Central Highlands fauna we thought that speciation within the clades inhabiting these regions might be due to Pleistocene glaciation. Glacial activity caused the regions to the north to become disjunct by depositing till and/or loess and silting of the streams in areas now referred to as the Central Lowlands. This might be termed the "Pleistocene hypothesis." The question is not whether the Illinoian (and probably the earlier Kansan) Glacier caused a

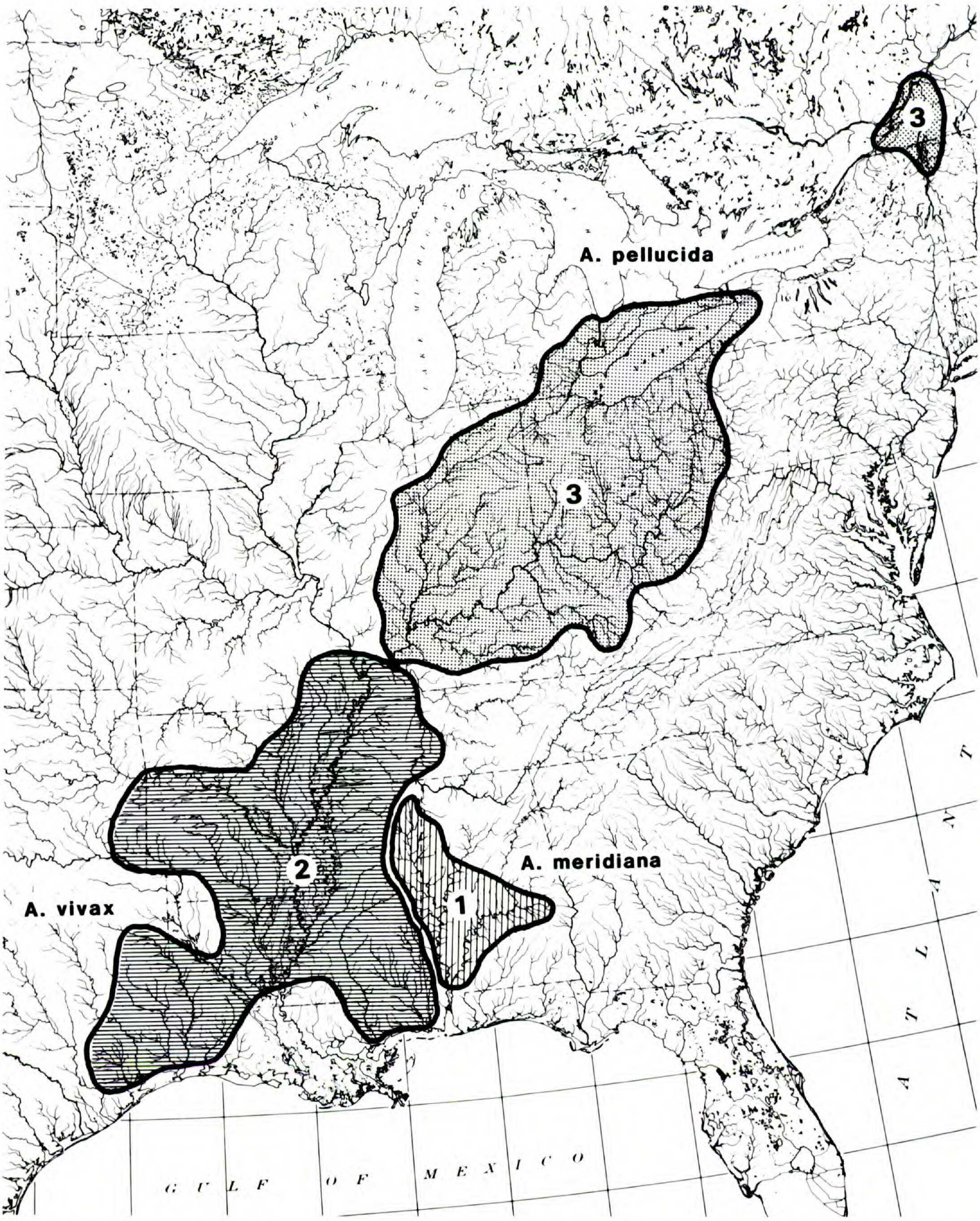

FIGURE 15. Distribution of the *Ammocrypta pellucida* species group (from Williams, 1975). Tree: 1+(2+3). Relationships discussed by Williams (1975).

disjunction. Rather, was some of the speciation within the Central Highlands fish fauna correlated with the event(s) or, were the species we observe today extant at the beginning of the Pleistocene and perhaps speciated, in a drainage system pattern that was subsequently replaced by the pattern we see today? This latter hypothesis might be termed the "pre-Pleistocene hypothesis."

Clades that conform to the Pleistocene hypothesis would be expected to show the following attributes: (1) they have one speciation event that

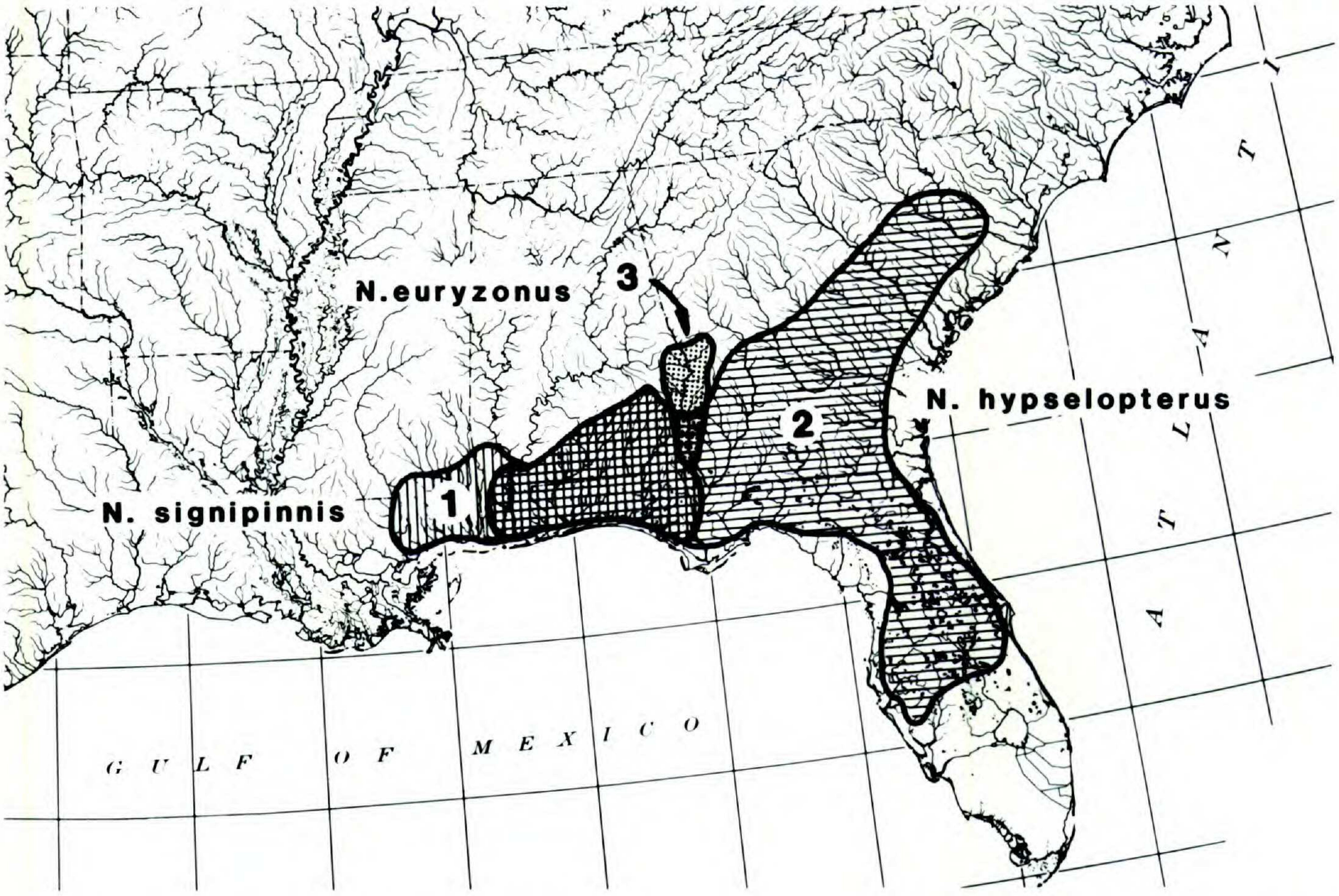

FIGURE 16. Distribution of the *Notropis hypselopterus* species group (from Gilbert & Platania, 1980). Tree: 1+(2+3). Characters supporting monophyly of the group: (1) very shallow preethmoid socket on the palatine, (2) presence of a broad lateral stripe on the body, and (3) iridescent colors (Mayden, unpubl. data). Characters supporting (2+3): breeding tubercles on mandibles directed laterally and in "comb" rows (Mayden, unpubl. data).

is congruent with the Interior-Tennessee disjunction, and (2) no speciation event within either region can be correlated with an event that was pre-Pleistocene or pre-Illinoian in origin. Three species groups conform to these attributes:

1. The *Notropis spectrunculus* species group (Fig. 29). A clade of two described and one undescribed species (Ramsey, 1965; Mayden, unpubl. data). Only the described species ranges are shown, the undescribed species is found in the Tennessee and Cumberland River systems and is the sister species of *N. spectrunculus* (Branson, 1983).
2. *Etheostoma niangue* and *E. saggita* (Fig. 30). Most workers (e.g., Bailey, 1948; Page & Whitt, 1973) have considered this pair sister species. Relationships to other members of the genus are not clear.
3. *Percina cymatotaenia* and *P.* sp. cf. *cymatotaenia* (Fig. 31) (Page, 1974, 1983).

This is not an impressive list. Further all three clades show wide geographic disjunctions between species that indicates much extinction and, in no case do we have the phylogenetic information necessary to relate any of these clades to other species within their genera. Finally, while they conform to our expectations regarding the Pleistocene hypothesis, they are also perfectly consistent with the pre-Pleistocene hypothesis.

Clades that conform to the pre-Pleistocene hypothesis may be expected to show the following attributes. (1) They contain one or more species in both the Interior and Tennessee Highlands and one or more additional species endemic to one of these regions, indicating that speciation in the clade and the achievement of sympatry occurred before the Pleistocene. (2) They contain a species (or more than one species) that has relict populations of early Pleistocene origin, dating that species as existing before Illinoian glaciation, the last known event to split the Central Highlands. (3) They contain species whose origin can be dated as early Pleistocene or pre-Pleistocene and who are of more recent origin than the taxa conforming to the disjunction between the Tennessee and Interior Highlands.

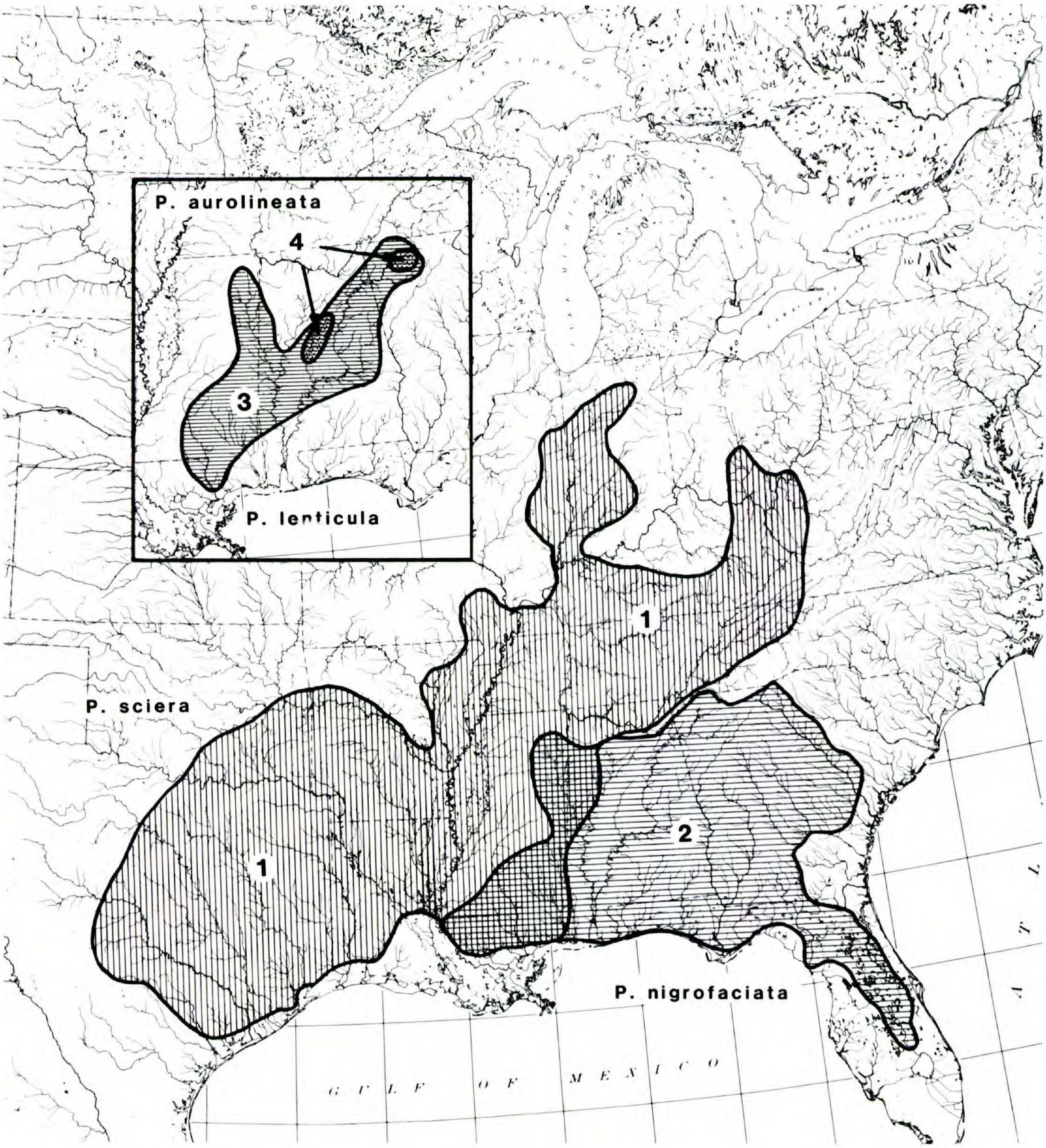

FIGURE 17. Distribution of the subgenus *Hadropterus*, genus *Percina* (from Page, 1974, 1983). Tree: 3+[4+(1+2)]. Characters supporting tree: see Page (1974).

Clades which have one or more of these attributes are listed below. The first five show attributes 1 and 2.

1. *Fundulus catenatus* species group (Fig. 32). *Fundulus catenatus* is found in both highland regions. *Fundulus stellifer* is probably its closest relative (Wiley, in press; data from Williams & Etnier, 1982), and the pair shows a highlands–Mobile Bay pattern similar to *Notropis leuciodes* and *N. chrosomus* (see below). *Fundulus catenatus* in the Interior Highlands comprises two populations, one in the Ozarks, another in the Ouachita Highlands. These highlands were once continuous but were dissected by the present Arkansas River *prior* to the Sangamonian, the interglacial just after the Illinoian Glacier (Quinn, 1958). In addition, there is one disjunct population in Indiana (?Illinoian relict) and at least one in Mississippi (age unknown).

2. The *Hybopsis dissimilis* group (Figs. 33, 34).

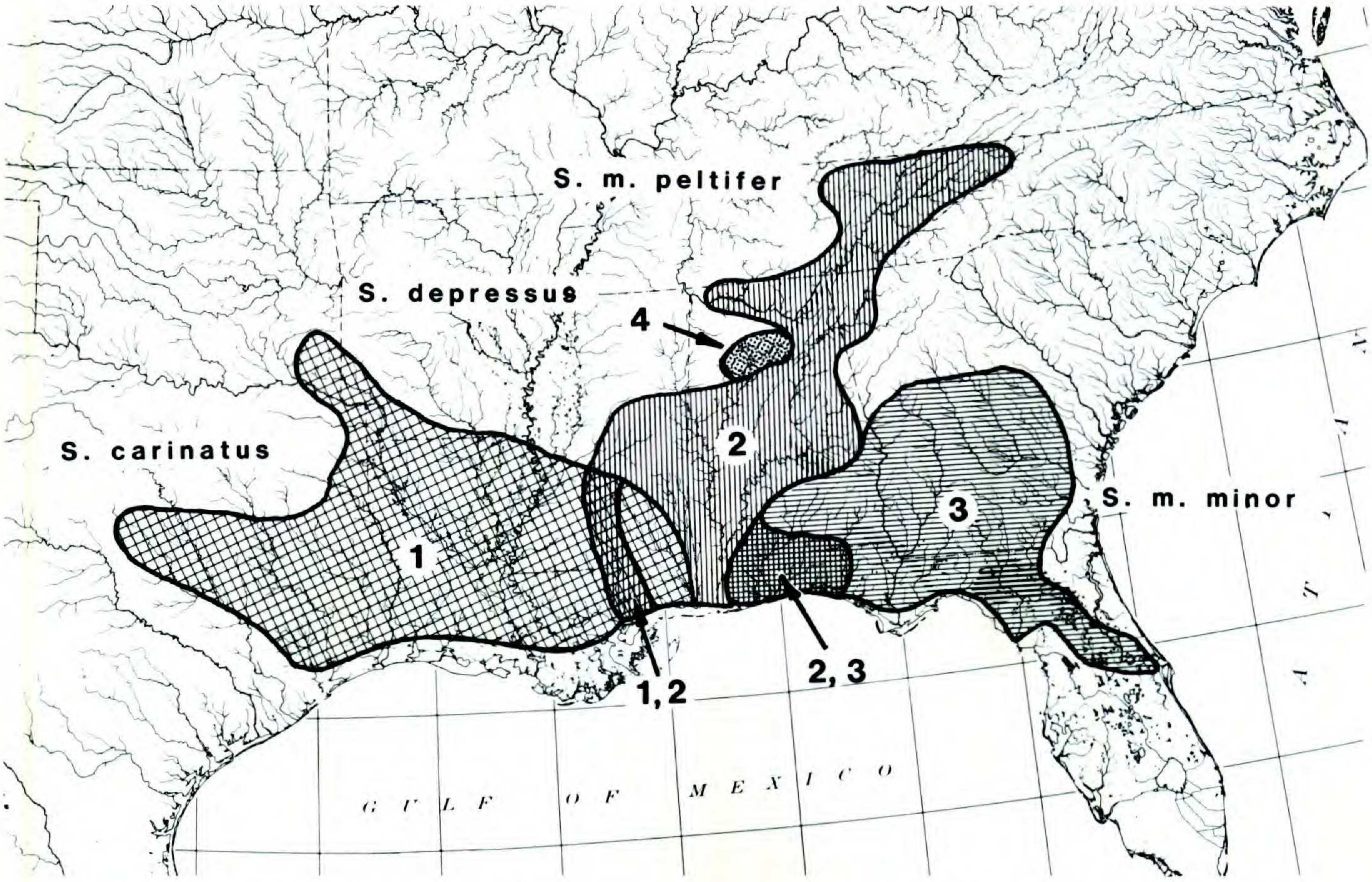

FIGURE 18. Distribution of three species of *Sternotherus* (from Tinkle, 1958). Tree: unresolved.

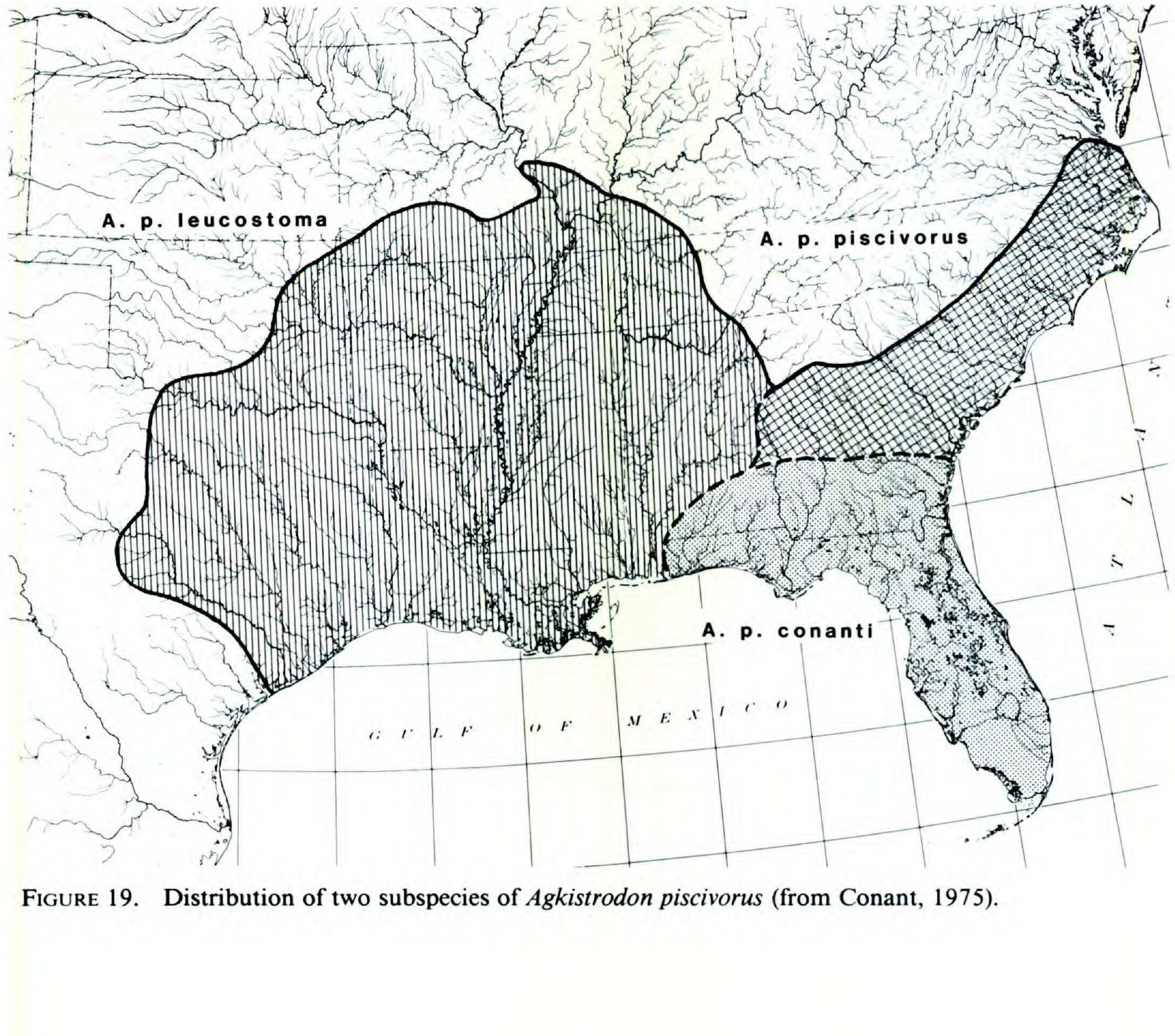

FIGURE 19. Distribution of two subspecies of *Agkistrodon piscivorus* (from Conant, 1975).

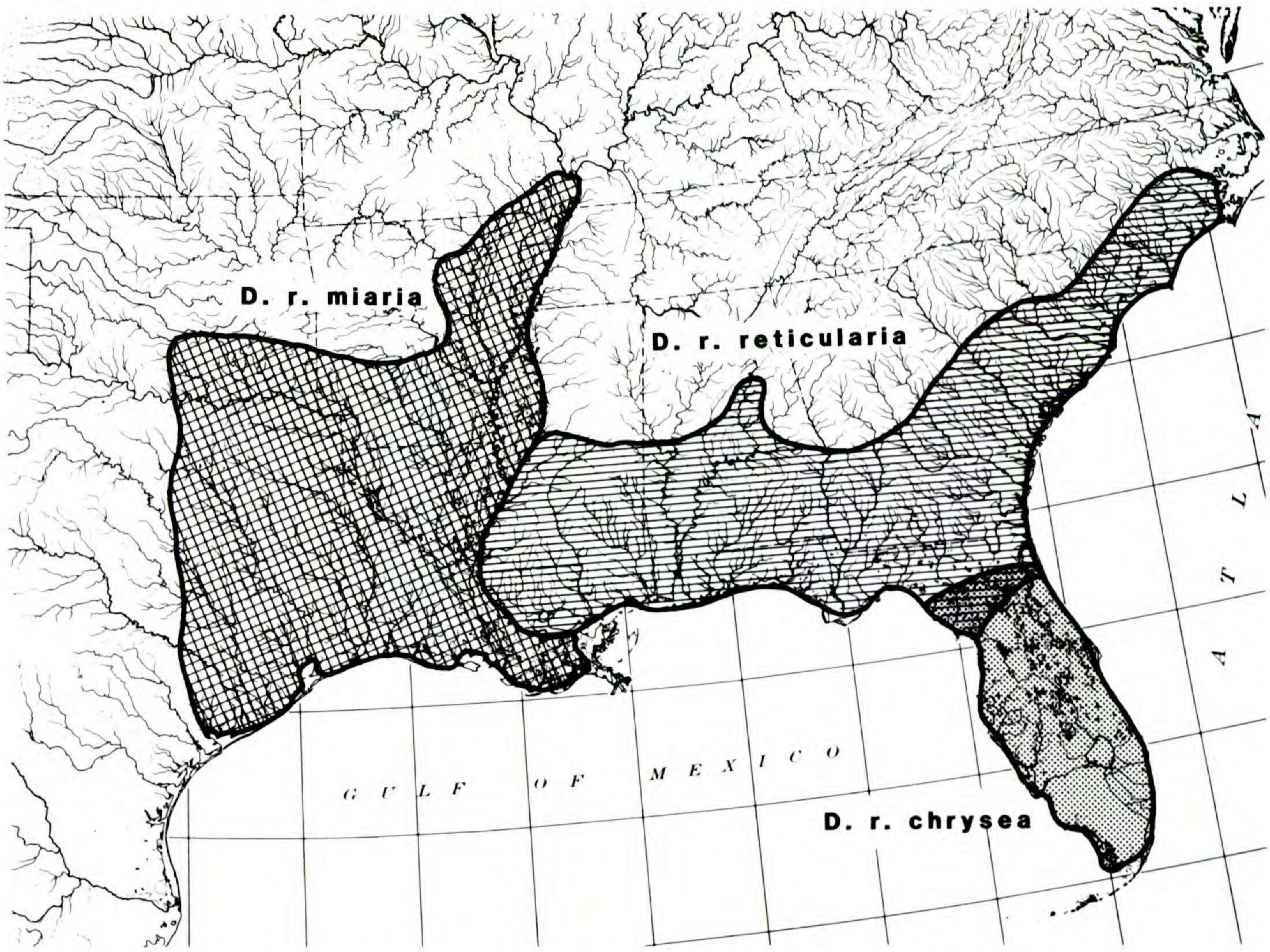

FIGURE 20. Distribution of three subspecies of *Deirochelys reticularia* (from Zug & Schwartz, 1971). Tree: unresolved.

This group contains five species of chubs characterized by having a unique barbel morphology (Mayden, unpubl. data). The species relationships are unanalyzed, but *H. insignis* and *H. dissimilis* share one derived character (presence of lateral pigment blotches on the flanks), which indicates they are sister species. *Hybopsis dissimilis* is found in both highland regions and is broadly sympatric with *H. insignis.* Further, *H. insignis* has a number of relict populations, some of which correspond to regions along the southern edge of the Illinoian Glacier. *Hybopsis x-punctata* is found in the Ozark Highlands and has several disjunct populations including one in the Ouachita Highlands, several north of the Ozarks and several congruent with the eastern disjunct populations of *H. dissimilis.*

3. The *Notropis telescopus* group (Fig. 35). This is a clade of four species, which includes two Eastern Highlands species (*N. semperasper* and *N. scepticus*) as well as two Central Highlands species (*N. telescopus* and *N. ariommus*) (Coburn, 1982). *Notropis telescopus* is found in both highland regions. *Notropis ariommus* is more closely related to the two Eastern Highland species and it has a number of disjunct populations in the Central Lowlands.

4. The *Notropis zonatus–coccogenis* group (Fig. 36). In this case we have five species and two clades (Buth, 1979; Buth & Mayden, 1981; Mayden, unpubl. data). The clades show the Interior-Tennessee split. However, only *N. coccogenis* is a Tennessee form and it is most closely related to *N. zonistius* from the Apalachicola River drainage. Further, *N. pilsbryi* is composed of three disjunct populations, one of which is confined to the Ouachita, dating it as pre-Sagamonian. Thus the origin of *N. zonatus* and *N. pilsbryi* must have occurred prior to this (unless *N. pilsbryi* is the ancestor of *N. zonatus*).

5. The *Notropis nubilus* group (Fig. 37). Three species are members of this clade (Swift, 1970). Two are found in the highlands and one in the Mobile Bay drainage. Relationships among the three are unresolved. If two highland species, *N. nubilus* and *N. leuciodus,* are closest relatives,

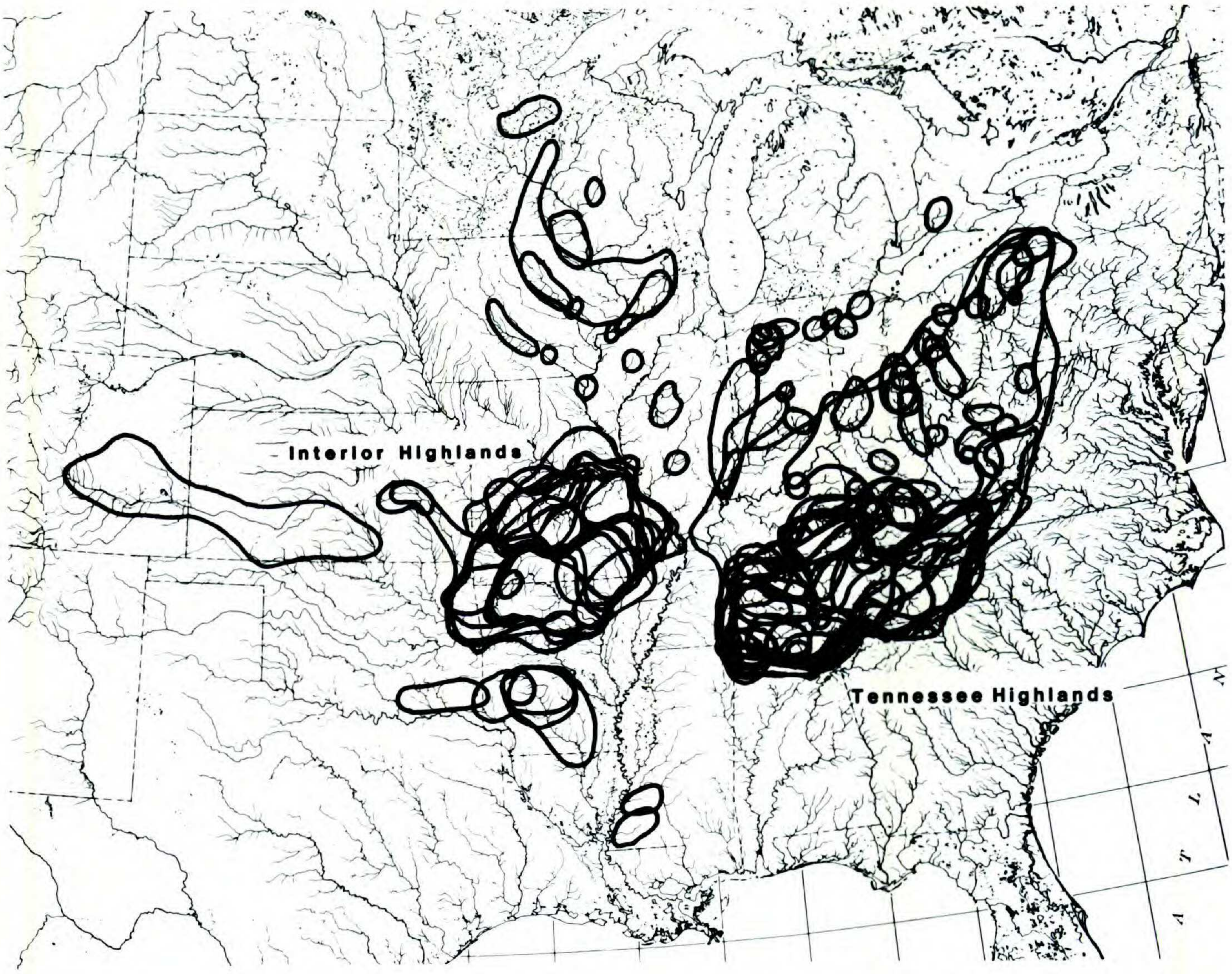

FIGURE 21. Composite ranges of 44 species of fishes largely confined to the Central Highlands of the United States, including disjunct populations found outside the region (mostly from Lee et al., 1980).

then the group would seem to be a candidate for the Pleistocene hypothesis. However, *N. nubilus* has a northern disjunct population that occurs, in part, in the "Driftless Area" of Wisconsin, Minnesota, and Iowa (Flint, 1957) and is probably a pre-Pleistocene relict (Pflieger, 1971). In addition, *N. nubilus* has a coiled gut found only in one other unrelated member of the genus (Swift, 1970; Snelson, 1971) indicating that it cannot be considered an ancestor that dispersed eastward during the Pleistocene to give rise to the eastern members of the clade.

6. The *Etheostoma variatum* group (Fig. 38). This group of darters comprises six species (Hubbs & Black, 1940; Richards, 1966; Mayden, unpubl. data). It is interesting because the Inte-

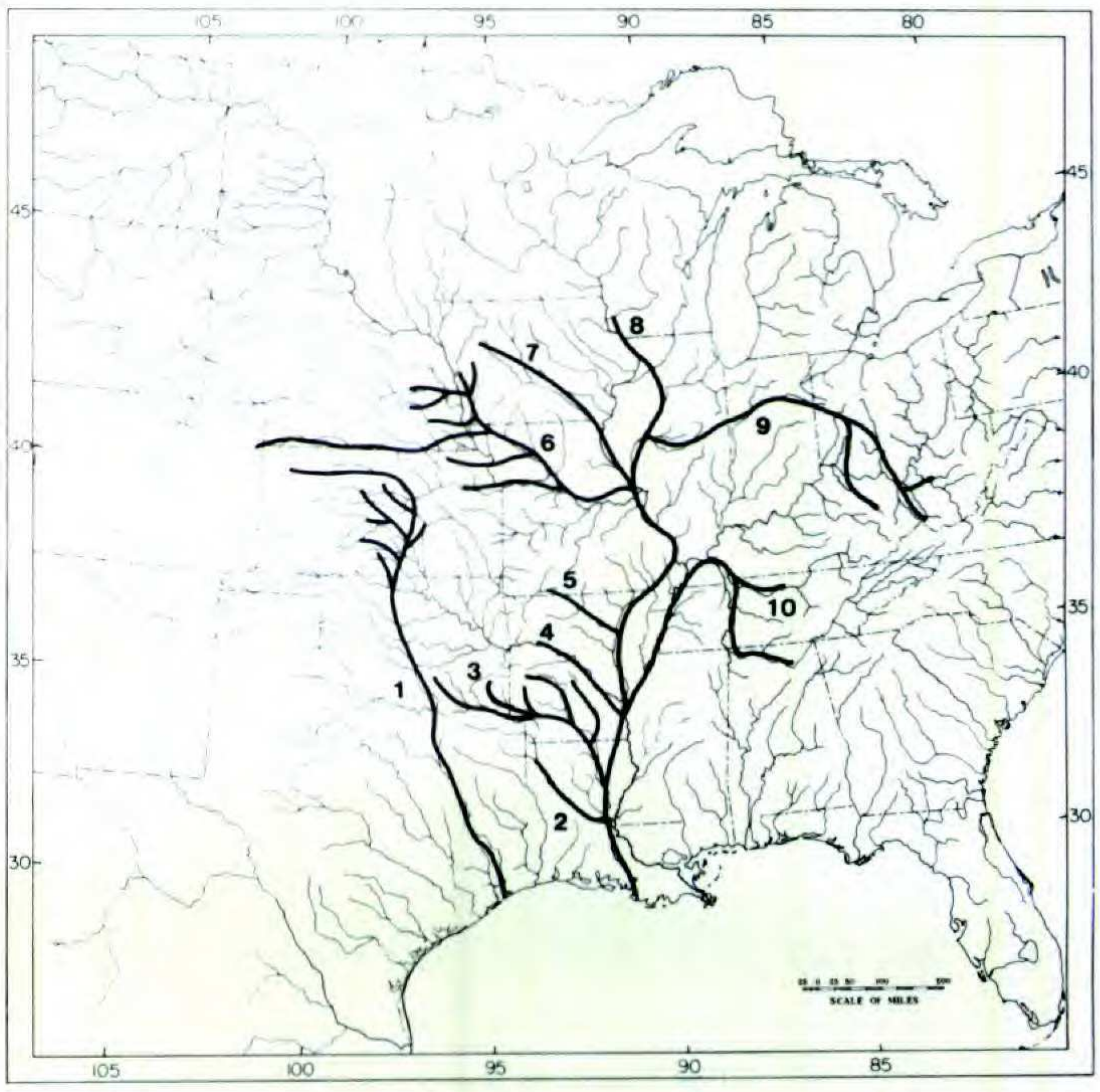

FIGURE 22. Pre-Pleistocene drainage patterns of the Central Highlands and adjacent regions. 1 = Plains Stream, 2 = Red River, 3 = Ouachita River, 4 = Arkansas River, 5 = White River, 6 = Grand River, 7 = Iowa River, 8 = upper Mississippi River, 9 = Teays River, 10 = Cumberland and Tennessee Rivers. (Modified from Mayden, 1985.)

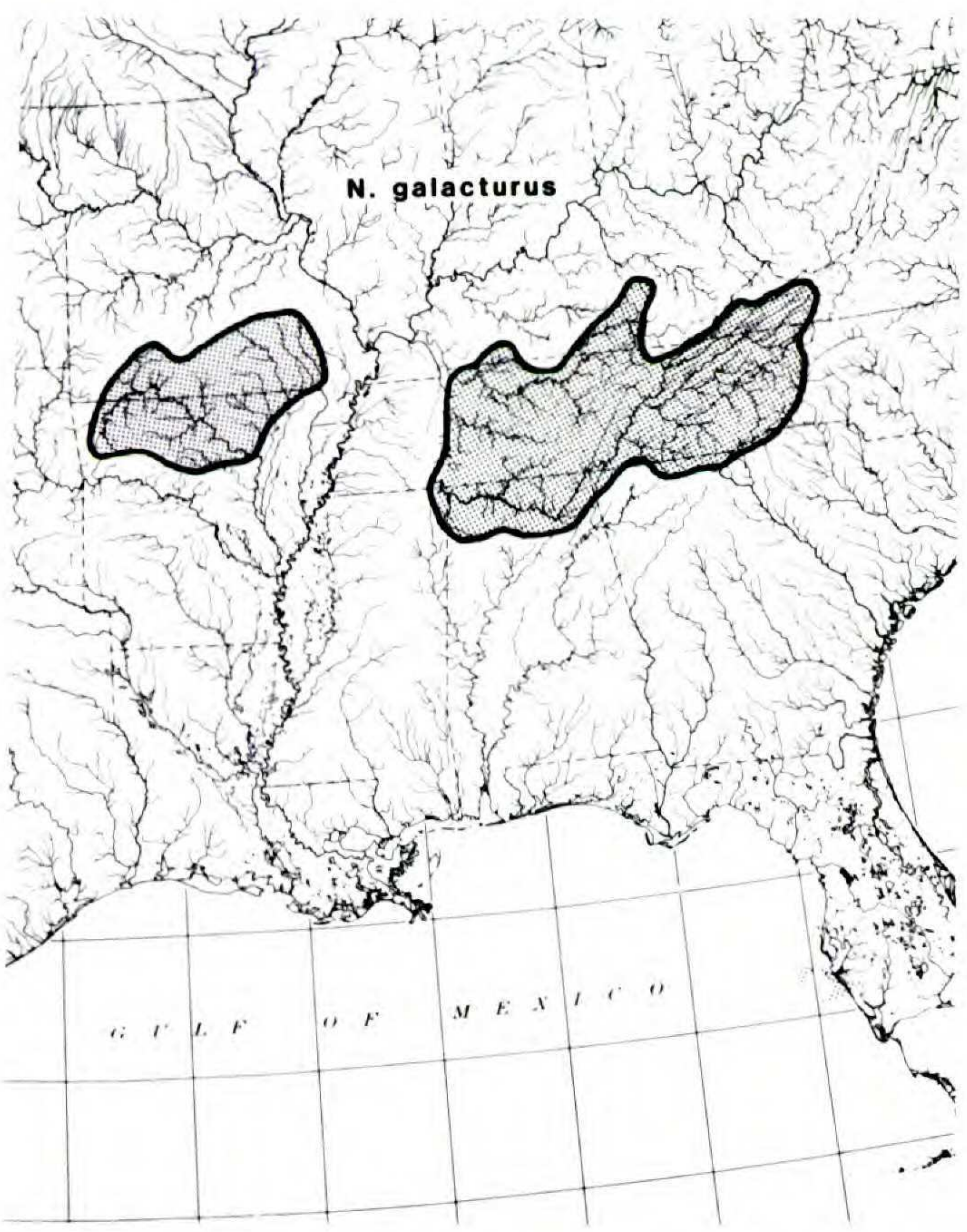

FIGURE 23. Distribution of *Notropis galacturus* (from Lee et al., 1980).

rior-Tennessee split does not correspond to two monophyletic groups. Rather, *E. blennius* is the oldest member of the group and there is evidence that there was a separation of the southern part of the Tennessee Highlands from the presumably continuous highland fauna to the north and west (essentially Tennessee River versus Teays-Mississippi). The next speciation event involved *E. sellare* and the ancestor of the remaining species and was a highlands versus East Coast vicariance event whose basis we cannot interpret (stream capture/peripheral isolation?). The remaining four species form a clade and have an Interior-Tennessee distribution. Whether the speciation event that separated members of this clade was the result of Pleistocene glaciation is problematical. However, we could resolve this by showing that the origin of the *E. osburni–E. kanawhae* species pair was early Pleistocene or pre-Pleistocene. Unfortunately there are no data concerning the age of the Kanawha Falls (Hocutt et al., 1978), the geological feature that marks the boundary between these species and their sister, *E. variatum*. Alternately we could test the hypothesis by dating the time of origin of *E. tetrazonum* and *E. euzonum*. Thus this clade may show "attribute 3" patterns, but this hypothesis awaits more data.

Other taxa are of interest. Five additional groups, one species of amphibian and four fish groups, deserve mention as possible examples pertinent to our analysis.

1. *Cryptobranchus alleganiensis* has an overall distribution similar to the *Etheostoma variatum* group. One subspecies *alleganiensis* is found in both highland regions and there is a disjunct population on the East Coast (Fig. 39).

The four fish groups comprise either a single species for which subspecies are recognized or several closely related species. Lack of phylogenetic hypotheses concerning their relationships precludes their use in the analysis.

2. The subgenus *Swainia,* genus *Percina* (Fig. 40). The group contains four highland darters (one undescribed) and a widespread species (*P. phoxocephala*) not confined to highland habitats (Page, 1974).
3. The *Etheostoma maculatum* species group (Fig. 41). This group is interesting in having highland species, disjunct populations of one species (*E. maculatum*), and a southern disjunct species found in the drainage adjacent to that containing the southern disjunct population of *Fundulus catenatus* (Williams & Etnier, 1982). Thus it contains species relevent to testing a Gulf Coastal Plain connection as well as a highlands connection.
4. *Etheostoma blennioides.* Several subspecies are recognized (Miller, 1968), and the distribution of these is similar to others included in the analysis.
5. *Cottus carolinae.* This species includes three highland subspecies and a subspecies endemic to the eastern Mobile Bay drainage (Lee et al., 1980).

Vicariance—the Central Highlands—discussion. The evidence we have presented indicates that speciation in highland fishes cannot be correlated with the vicariance of the Central Highlands by the Illinoian Glacier. Rather, the evidence indicates that most or all of the species analyzed were present and living in the region before the Pleistocene and thus speciated over a landscape including drainage patterns not found today. Our data are not consistent with the idea that most of the groups analyzed lived north of their present distribution and were pushed south by glaciers to inhabit their present ranges, because several clades have relatives in the Coastal Plain (Mobile and Apalachicola drainages) and some have relatives on the Atlantic slope. This implies a history of contact between the high-

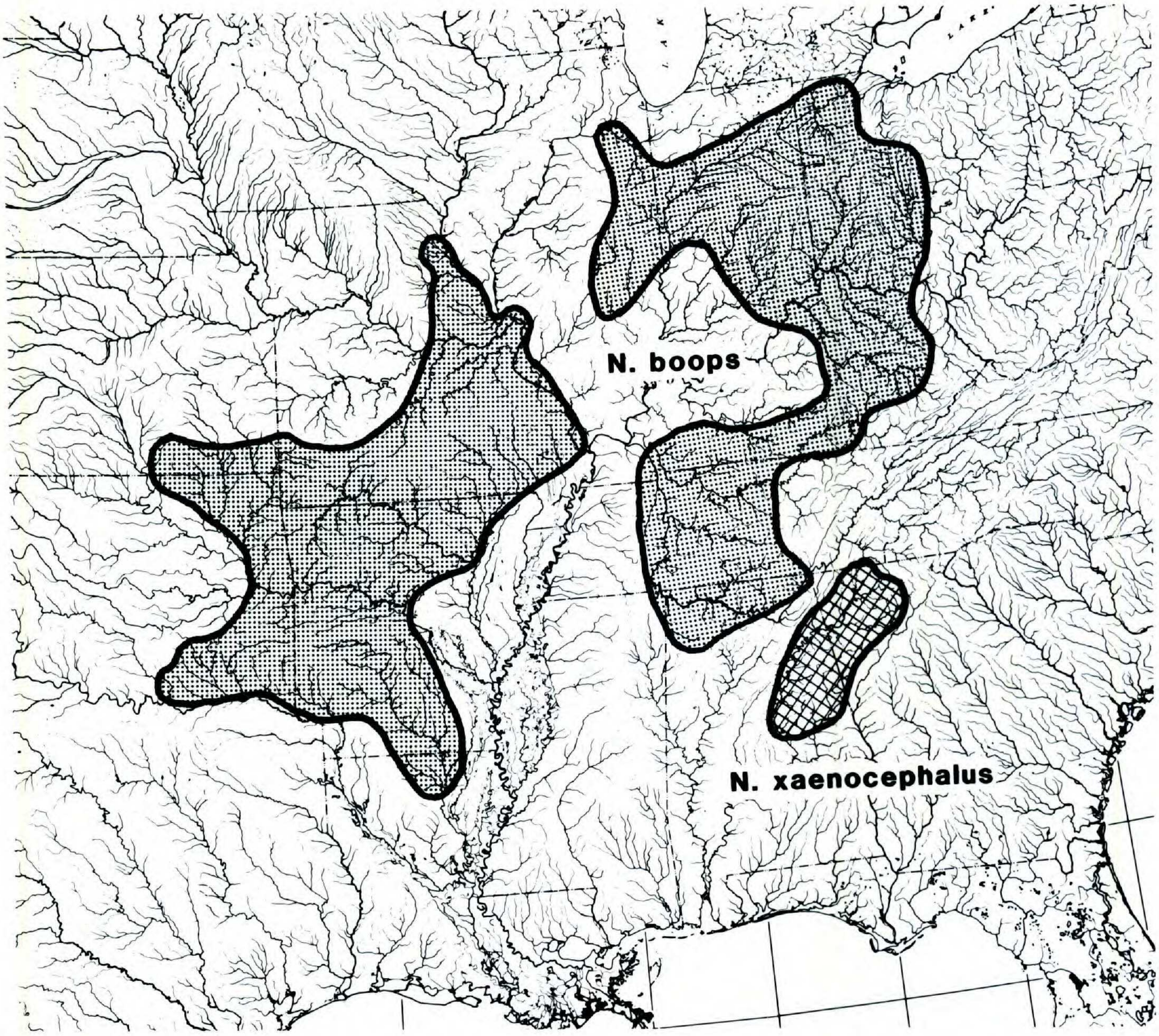

FIGURE 24. Distribution of *Notropis boops* and *N. xaenocephalus* (from Burr & Dimmick, 1983).

lands and the Gulf Coastal Plain. We *do not* wish to imply that the present disjunction is not correlated with the Illinoian Glacier. It probably did cause the disjunction we now observe by modifying the area north of the present highlands into the Central Lowlands. Further, we *do not* wish to imply that some speciation within either the Interior Highlands or the Tennessee Highlands had no correlation with Pleistocene events. It probably did. What we do wish to imply is that the simplest explanation for speciation observed in three species pairs we first discussed is not corroborated when we analyze the fauna as a whole. While large-scale vicariance speciation (Model I) might explain much of the evolution in the clades we have analyzed, glaciation does not provide a simple causal mechanism of vicariance correlated with speciation.

ALLOPATRIC SPECIATION II—PERIPHERAL ISOLATION

Peripheral isolation models postulate the origin of a new species in a very small portion of the range of an ancestor or colonization and subsequent differentiation of a part of the earth not occupied by the ancestor. One problem with deducing phylogenetic and biogeographic predictions from this mode is that there are at least two different processes that may be involved. In the case of what might be called "classic" peripheral isolation, the model invoked has a distinct ecological component as well as a historical component. New species arise in marginal habitats, usually but not always at the periphery of the ancestral range. This is the model favored by Mayr (1963), Hennig (1966), and Brundin (1966).

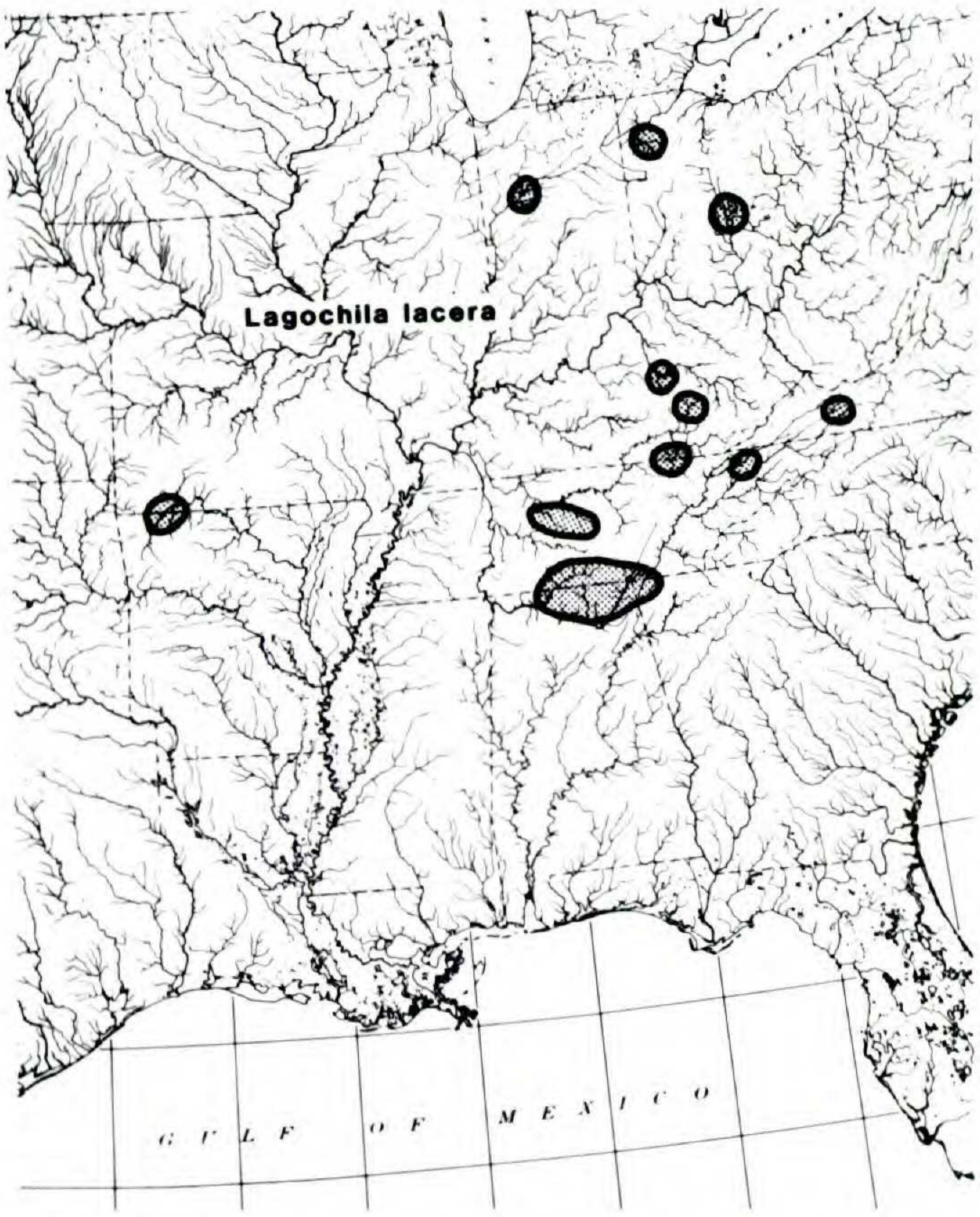

FIGURE 25. Known collection localities of *Lagochila lacera* (now extinct, from Lee et al., 1980).

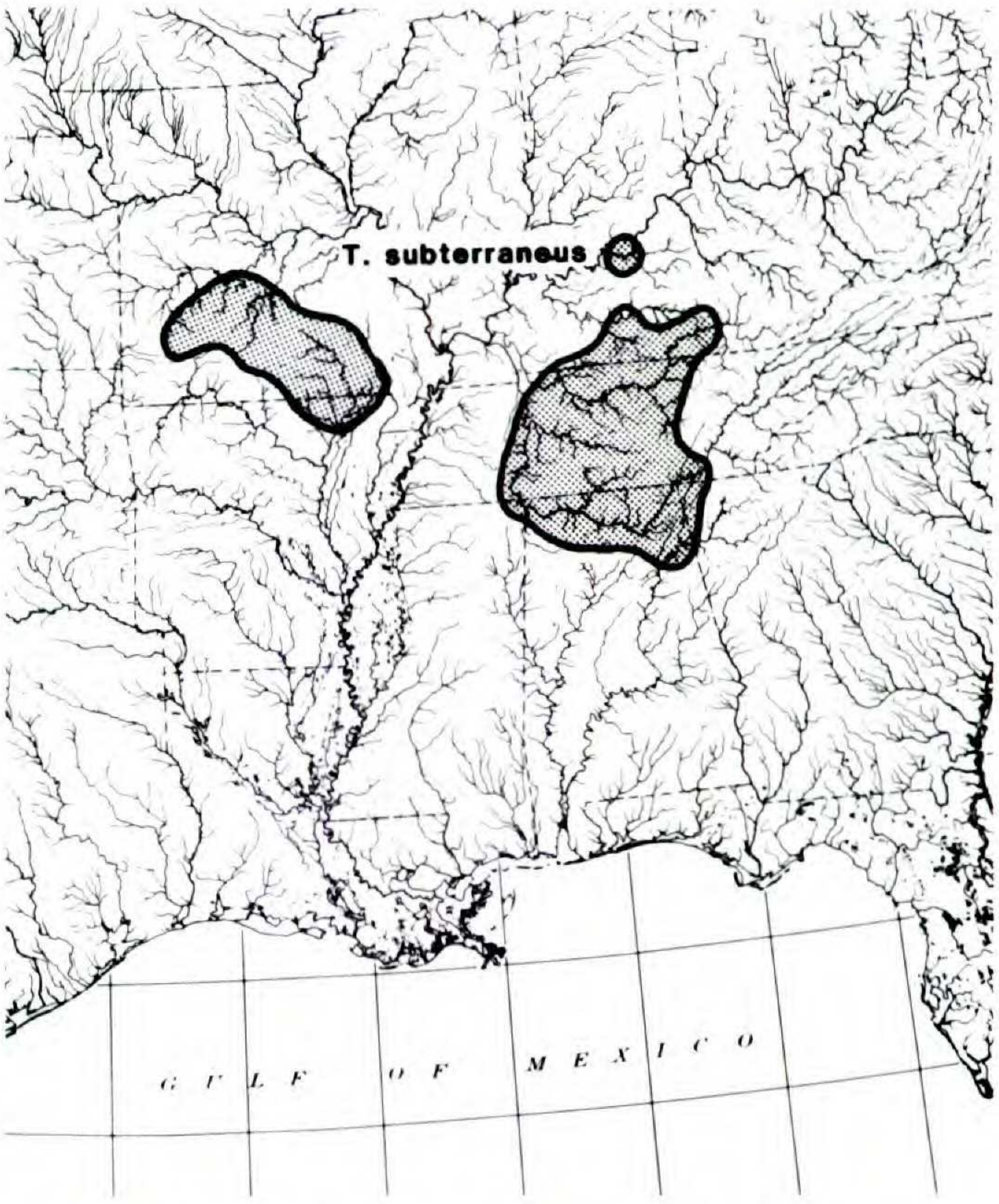

FIGURE 26. Distribution of *Typhlichthys subterraneus* (from Lee et al., 1980).

It includes the notion that populations inhabiting marginal areas are somewhat free to diverge from the central population because of decreased gene flow. At least some, including Hennig (1966), also assert that differentiation occurs in response to the different ecological conditions encountered by the isolated population.

In "vicariant" peripheral isolation, the model invoked has a historical component but not necessarily an ecological component. It is simply the end of a continuum of possibilities for subdividing an ancestral species, with large-scale vicariance involving large chunks of range and peripheral isolates involving very small chunks.

The commonality shared by these two types of peripheral isolation concern the characteristics of the ancestor relative to the descendant. Specifically, the ancestor is thought to survive the speciation event unchanged or largely unchanged, whereas the peripheral isolate diverges (cf. Mayr, 1963; Grant, 1971; Eldredge & Gould, 1972). Whether or not the ancestor "really survives" is not the issue, rather, the issue is whether the large population evolves to any significant degree in a manner correlated with the speciation event. When we say "really survives" we refer to various metaphysical arguments dating to Hennig's (1966) methodological conclusion that ancestral species always go "extinct" at branch points. We do not believe it is necessary to postulate this. Without arguing the merits of the metaphysical case (we have no stake in the outcome of such an argument), the hypothesis is clear. Hennig's (1966) deviation rule applies. One species, the peripheral isolate, diverges more from the ancestral condition than the other. A variety of predictions can be generated under this model (or models). These fall into two general classes, predictions from single speciation events and predictions from multiple speciation events.

Peripheral isolation—single speciation events. Peripheral isolation involving one central population and one peripheral population results in a dichotomous tree at the level of species. Thus the tree pattern is identical to that produced by large-scale vicariance. The biogeography, however, is quite different. We would expect the speciation event to result in a biogeographic topology of a widespread species and a species of very limited range. For example, in the North American killifish genus *Fundulus*, *F. diaphanus* is a wide-ranging species and its sister species, *F. waccamensis*, is restricted to Lake Waccamaw in North Carolina, and one artificially introduced population (that can be ignored) found in Phelps Lake, North Carolina. In describing *F. waccamensis*, Hubbs and Raney

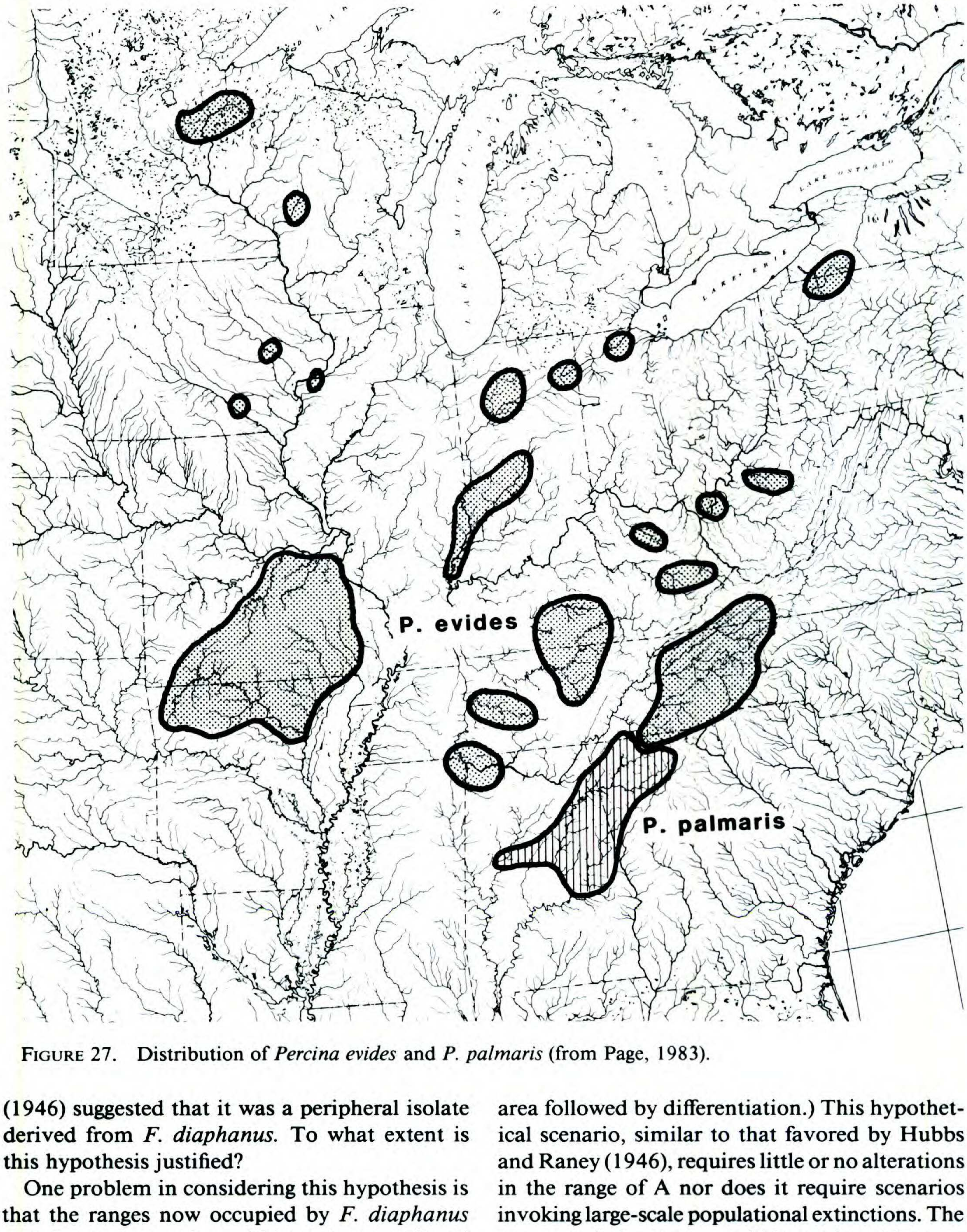

FIGURE 27. Distribution of *Percina evides* and *P. palmaris* (from Page, 1983).

(1946) suggested that it was a peripheral isolate derived from *F. diaphanus*. To what extent is this hypothesis justified?

One problem in considering this hypothesis is that the ranges now occupied by *F. diaphanus* and *F. waccamensis* could have been achieved in several different ways. In Figure 42a we show the geographic relationships between two hypothetical species, A and B. In Figure 42b we show the origin of B as a peripheral isolate derived from a "small-scale" vicariance event. (The same effect would be achieved by dispersal of one or more populations ancestral to B into the area followed by differentiation.) This hypothetical scenario, similar to that favored by Hubbs and Raney (1946), requires little or no alterations in the range of A nor does it require scenarios invoking large-scale populational extinctions. The same result, however, could be achieved by very different scenarios, three of which are shown in Figure 42c, d, and e. These include (1) peripheral isolation of A with subsequent displacement of B into its present range (Fig. 42c), (2) a large-scale vicariance event resulting in the origins of both A and B, with subsequent displacement of B (Fig. 42d), and (3) widespread extinction of the

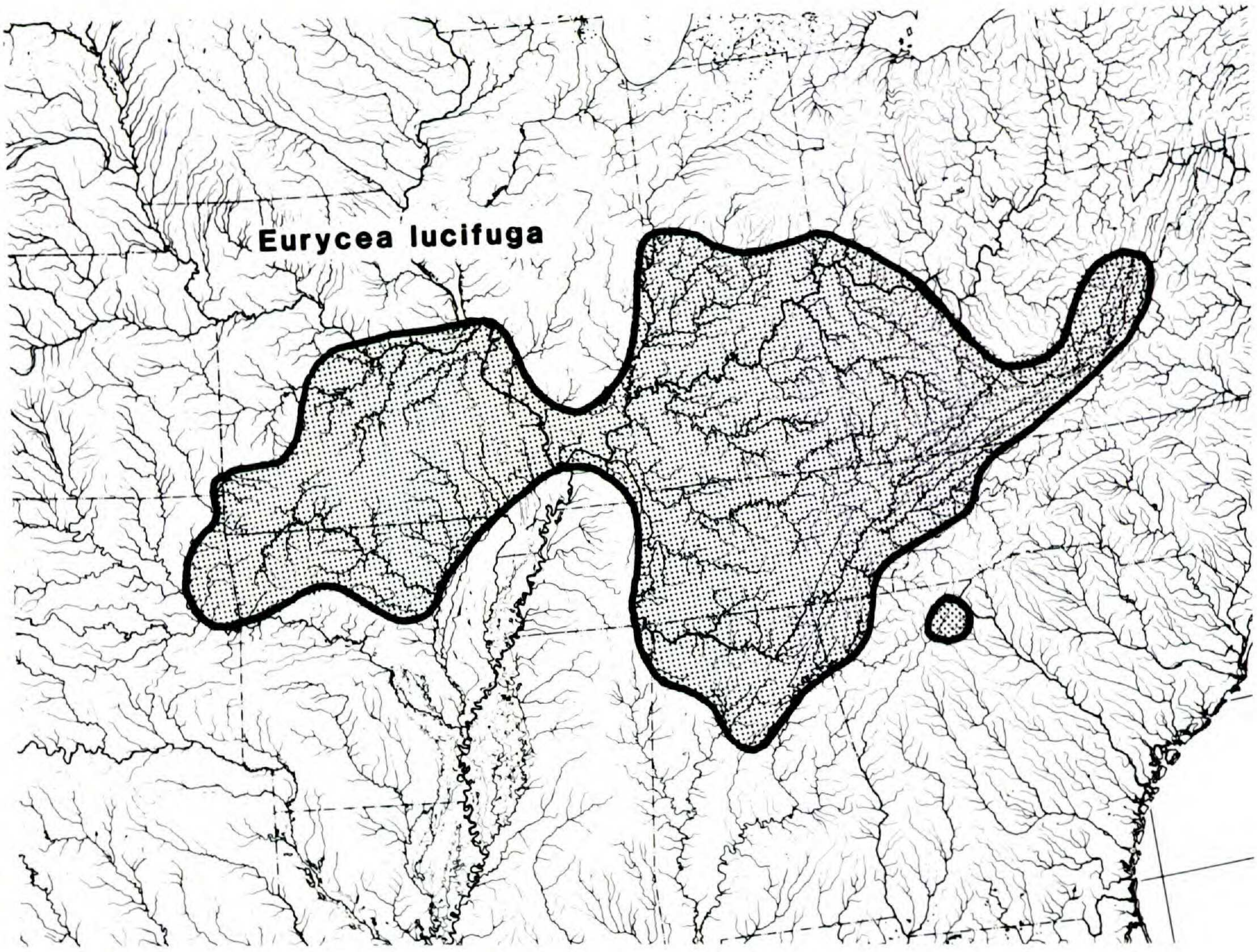

FIGURE 28. Distribution of *Eurycea lucifuga* (from Conant, 1975).

original ancestral populations with both A and B originating in the resulting refugia, followed by a re-invasion of the original range of the ancestor by A (Fig. 42e). The problem is—how can we sort out these four very different scenarios?

One rather direct approach might be to adopt a parsimony argument and claim that it is simpler to adopt a model that requires no extinctions or dispersal (i.e., Fig. 42b) because such a model contains the fewest *ad hoc* assumptions. We would reject this purely logical approach for two reasons. First, parsimony is a logical device and cannot be used to test a proposition. It proceeds by weighing conflicting data and there are none. Second, the importance (or lack thereof) ascribed to this model of speciation by some make it important enough to be approached with some caution.

We suggest that certain lines of evidence might be developed. Some are "extrinsic" in that they deal with data concerning the histories of the respective geographic areas inhabited by the species involved. Some are "intrinsic" in that they deal with data derived from the species themselves.

Extrinsic evidence might take several forms. We might demonstrate that there is no evidence for climatic change or large-scale vicariance events occurring in the region presently inhabited by species A that would have effected it or its ancestor. This would reinforce the idea that neither Figure 42d nor e are applicable. We might find that the region occupied by species B either did not exist or was uninhabitable in the recent past, requiring a hypothesis of dispersal into the area. We might be able to identify a "small-scale" vicariance event with the isolation of the ancestral populations of B.

Intrinsic evidence is more difficult to speculate about, because the kinds of data derived from character analysis may depend on levels of gene flow between populations, the time that has passed since vicariance or dispersal, the history (or lack thereof) of gene flow between the isolate and the central population, and the effect (or lack

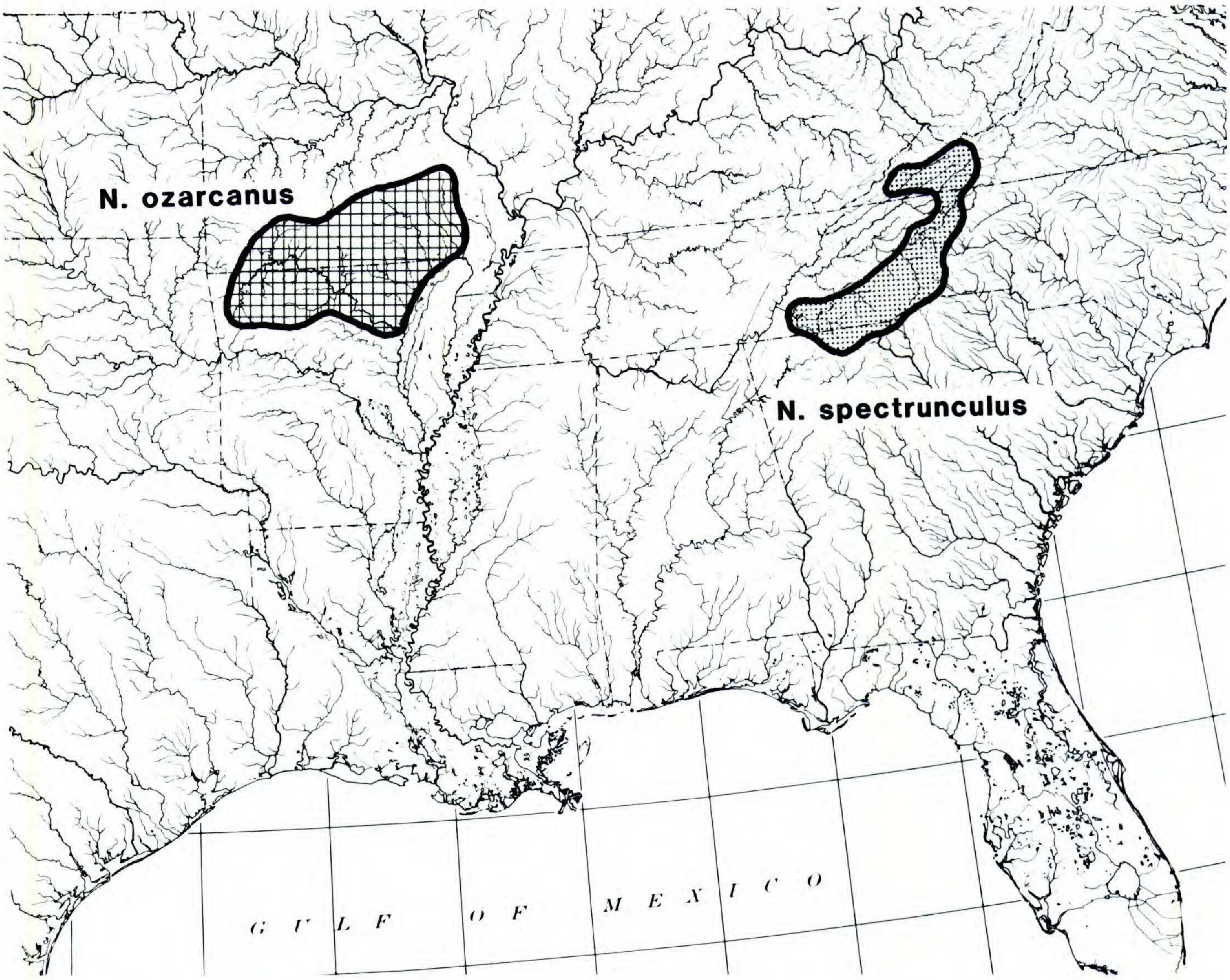

FIGURE 29. Distribution of the *Notropis spectrunculus* species group (from Ramsey, 1965; Mayden, unpubl. data). An undescribed species reported by Branson (1983) is found west of the range of *N. spectrunculus* and it is partly sympatric with this species. We have not plotted the range of the undescribed species for lack of distributional data.

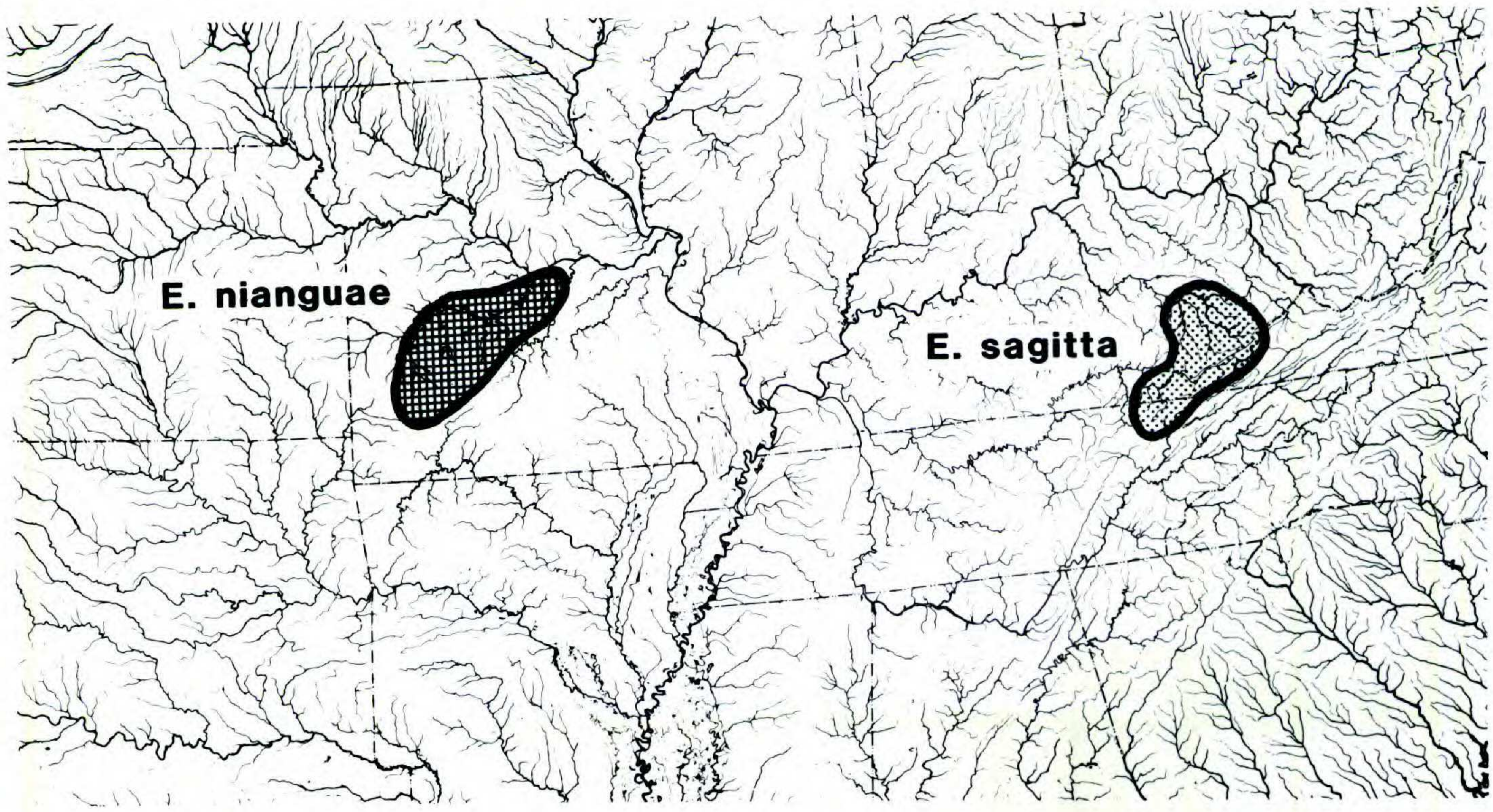

FIGURE 30. Distribution of *Etheostoma niangue* and *E. sagitta* (from Page, 1983).

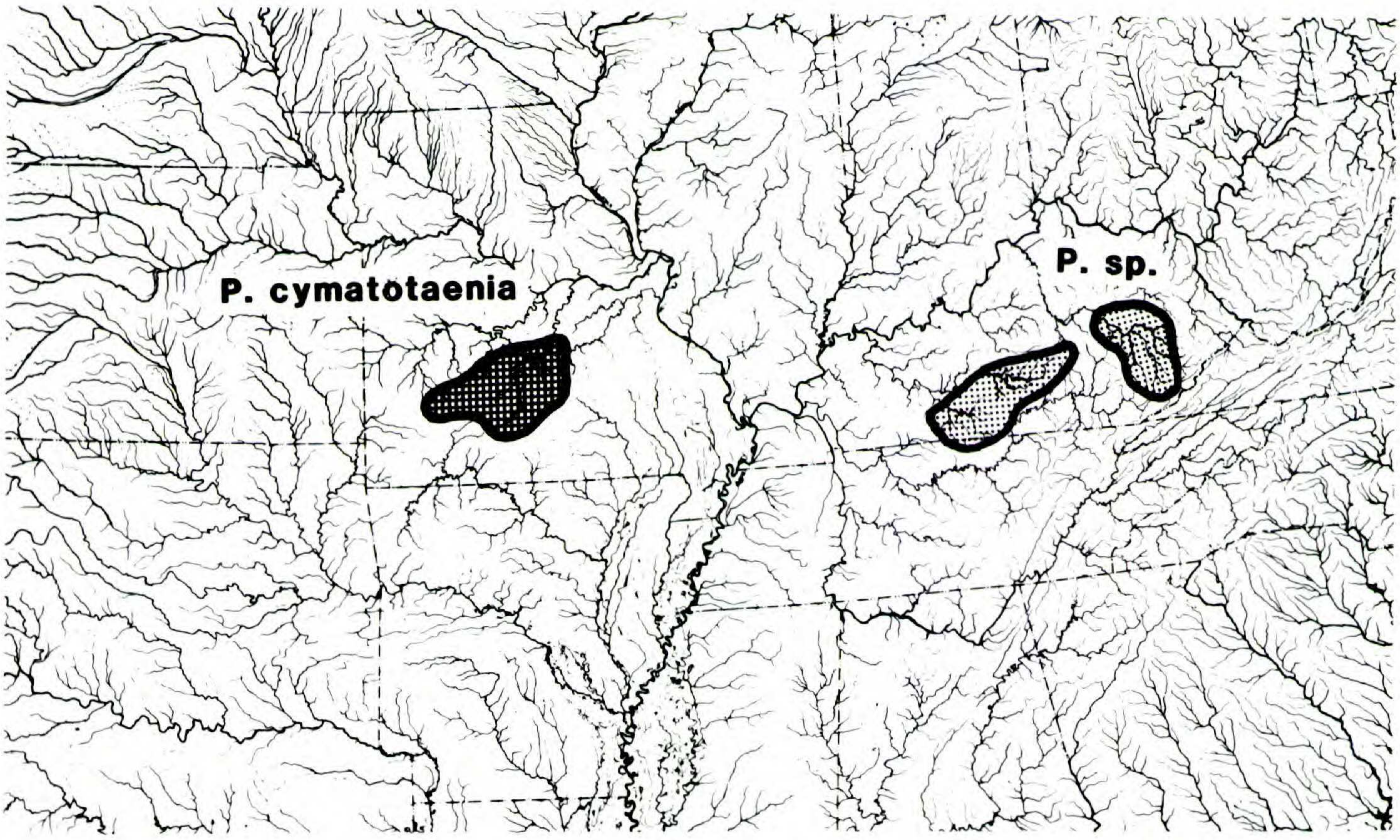

FIGURE 31. Distribution of *Percina cymatotaenia* and an undescribed sister species (from Page, 1983).

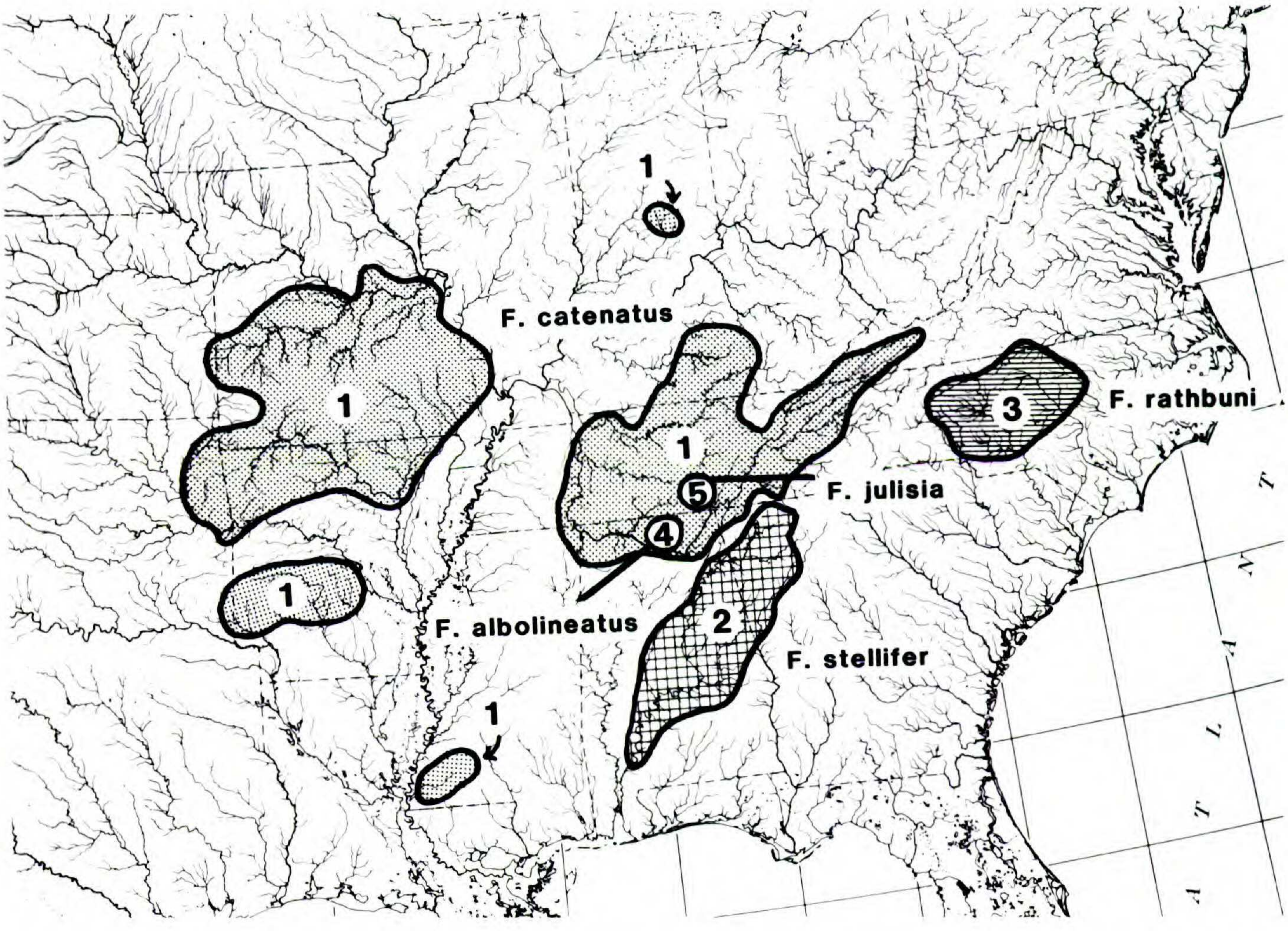

FIGURE 32. Distribution of the *Fundulus catenatus* species group (from Lee et al., 1980 and Williams & Etnier, 1982). Tree: 3+[4+5+(1+2)]. Characters supporting tree: see Wiley (in press).

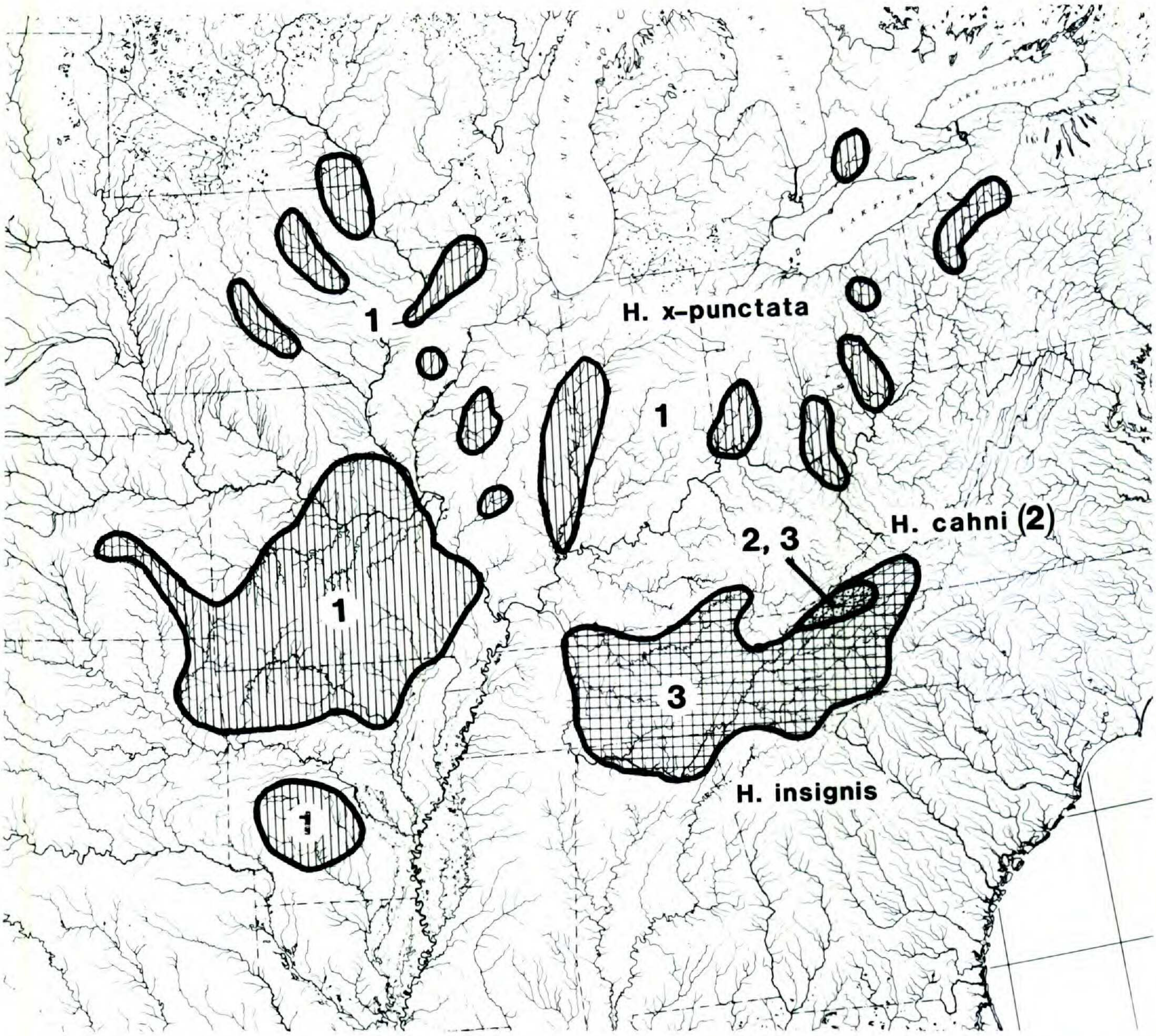

FIGURE 33. Distributions of some of the members of the *Hybopsis dissimilis* species group (from Lee et al., 1980). See Figure 34 for tree and characters supporting the tree.

thereof) of local selection on each population. Controversies exist concerning the population genetical aspects of founder effects and even the importance of peripheral isolation as a mechanism of speciation (for recent contrasting reviews see Carson & Templeton, 1984, and Barton & Charlesworth, 1984). In spite of these problems, we believe that certain lines of inquiry might be fruitful.

One line of inquiry might be developed around the notion that peripheral isolates diverge more than the central population. In a two-species system we might observe more fixed differences in the putative peripheral isolate relative to the reconstructed ancestral phenotype or genotype. For this to count, however, we would have to assume that the characters examined represent a random sample of all characters that have diverged. Further, lack of a sharp deviation (that is, the presence of equal divergence in both lineages) might be compatible with peripheral isolation if the two species are of sufficiently ancient origin (thus providing time for anagenesis in the wide-ranging species) and the wide-ranging species is characterized by high levels of gene flow (thus providing the opportunity for the spread of evolutionary novelties).

Another line of evidence might be developed by considering the geographic variation of certain kinds of characters. If species B is a peripheral isolate, it was probably derived from populations of A near its range or, alternately, was in genetic contact with such populations before vicariance. This is probable if the scenario presented in Figure 4b is true. Rapidly evolving systems, especially if they were immune from se-

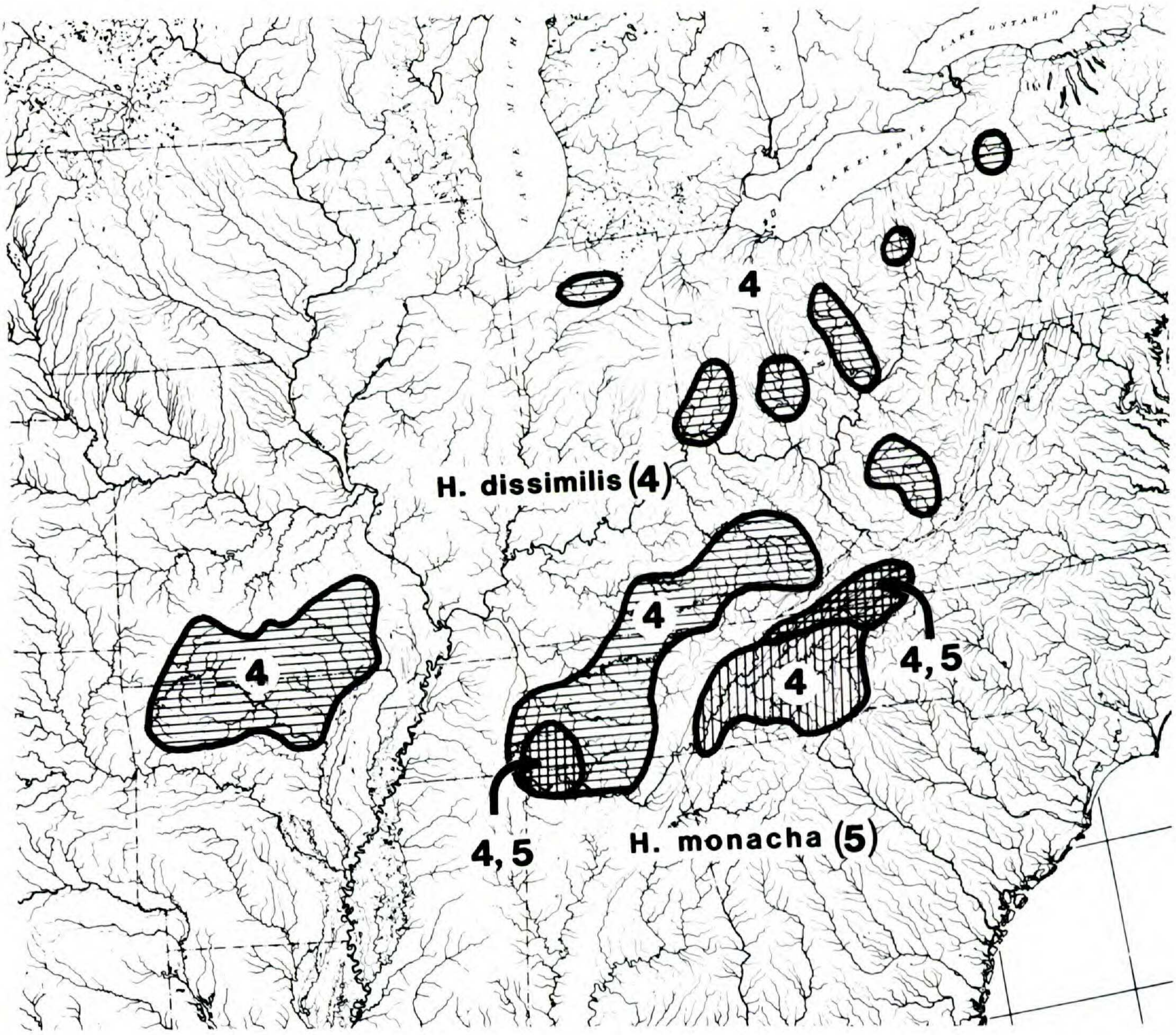

FIGURE 34. Distribution of the remaining species of the *Hybopsis dissimilis* species group (from Lee et al., 1980). Tree: 3+4+5+(1+2). Characters supporting monophyly of the group: (1) an elongate basihyal, (2) stellate barbel morphology, (3) high vertebral count. Character supporting (1+2): distinct lateral blotches on the side of the body. (Characters from Mayden, unpubl. data.)

lection and recombination, might show this relationship if a cladistic analysis was performed on geographic samples of populations of A and B. Mitochondrial DNA has the kinds of evolutionary characteristics suitable for such an analysis (Avise et al., 1979).

Another line of evidence might be developed by considering "ancestral clines," i.e., clines apparently present in ancestors that are retained in descendants (Wiley, 1981). At this level of analysis, does the putative peripheral isolate fit into the pattern of geographic variation exhibited by populations of the supposed ancestor? If so, can we use this as evidence to prefer the scenario in Figure 42b relative to the alternatives? Perhaps if we can show that the characters are derived and heritable or that the pattern indicates a past history of genetic contact, then the species pair is a good candidate for the peripheral hypothesis.

Returning to the *F. diaphanus–E. waccamensis* problem, we note the following. In terms of extrinsic evidence (1) Lake Waccamaw did not exist in the Middle Pleistocene. Thus its present freshwater fish fauna is the result of a colonizing event. (2) The lake is unique ecologically, being a clear, spring-fed lake surrounded by a tannic acid aquatic environment typical of the area. In terms of intrinsic evidence we note that while no detailed analysis of geographic variation has been published, *F. diaphanus* is comprised of two recognized subspecies connected by a zone of integration. The eastern form is "more similar" to *F. waccamensis* than is the northwestern form. Thus what we know about the relationships of

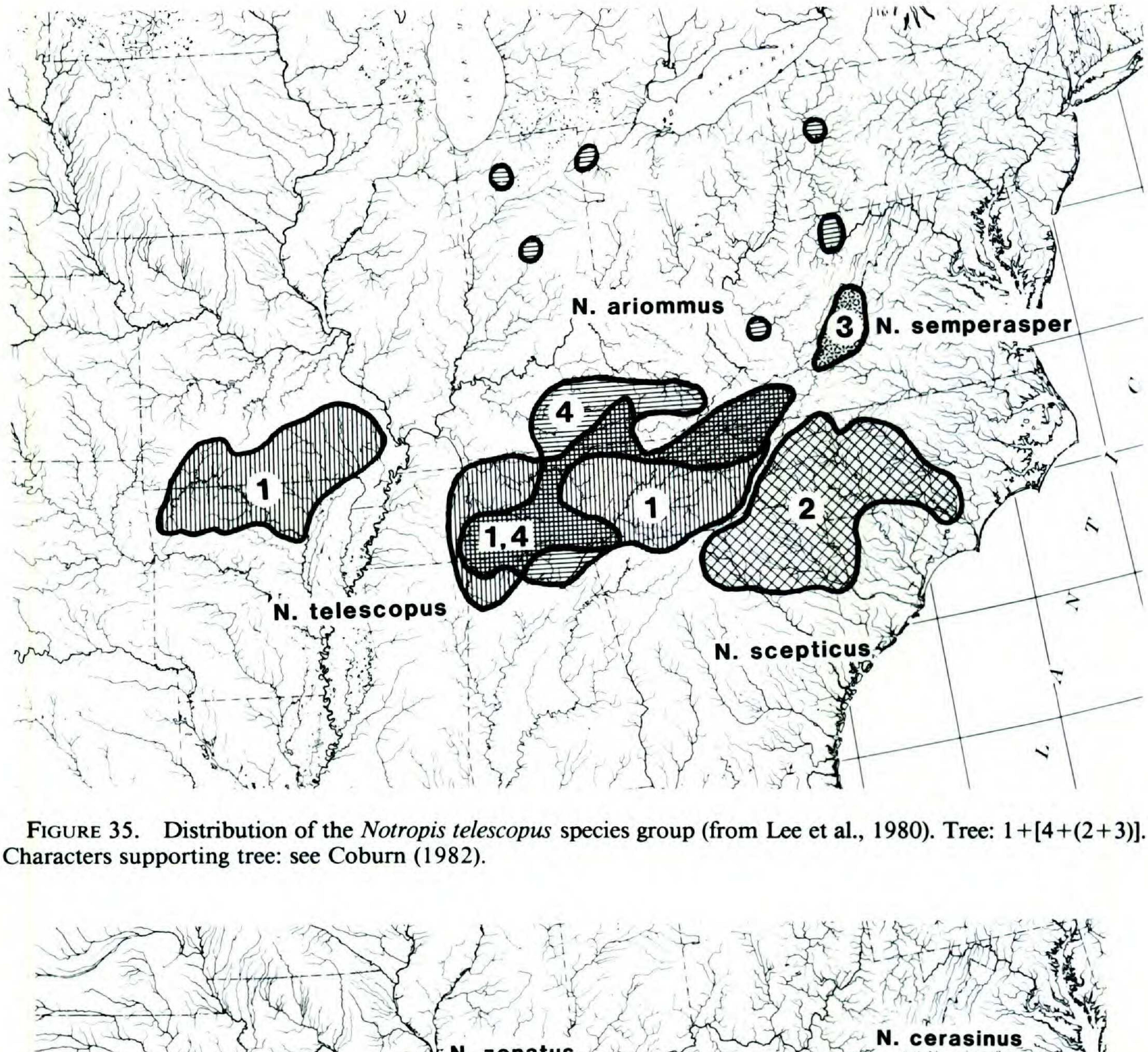

FIGURE 35. Distribution of the *Notropis telescopus* species group (from Lee et al., 1980). Tree: 1+[4+(2+3)]. Characters supporting tree: see Coburn (1982).

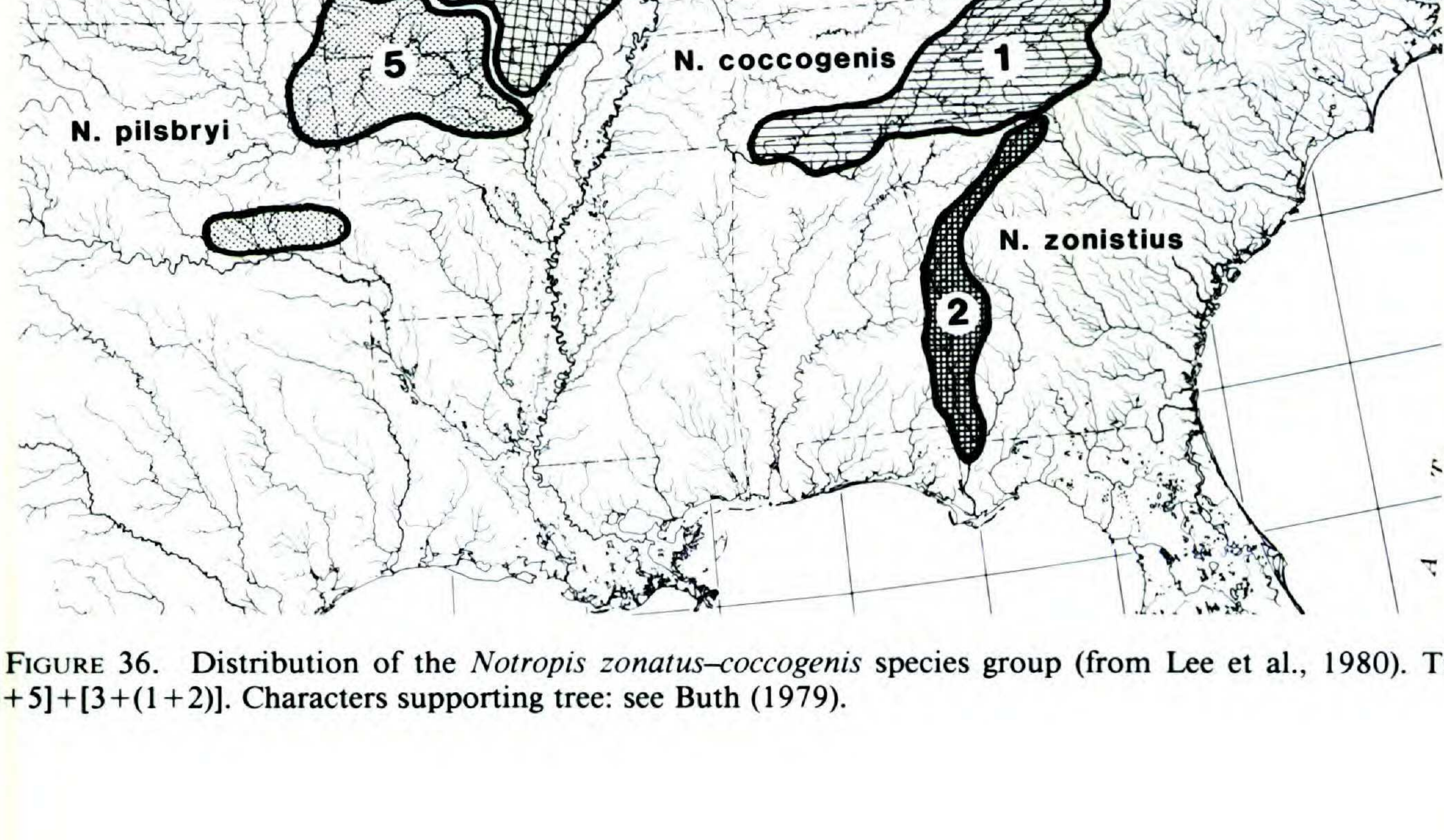

FIGURE 36. Distribution of the *Notropis zonatus–coccogenis* species group (from Lee et al., 1980). Tree: [4+5]+[3+(1+2)]. Characters supporting tree: see Buth (1979).

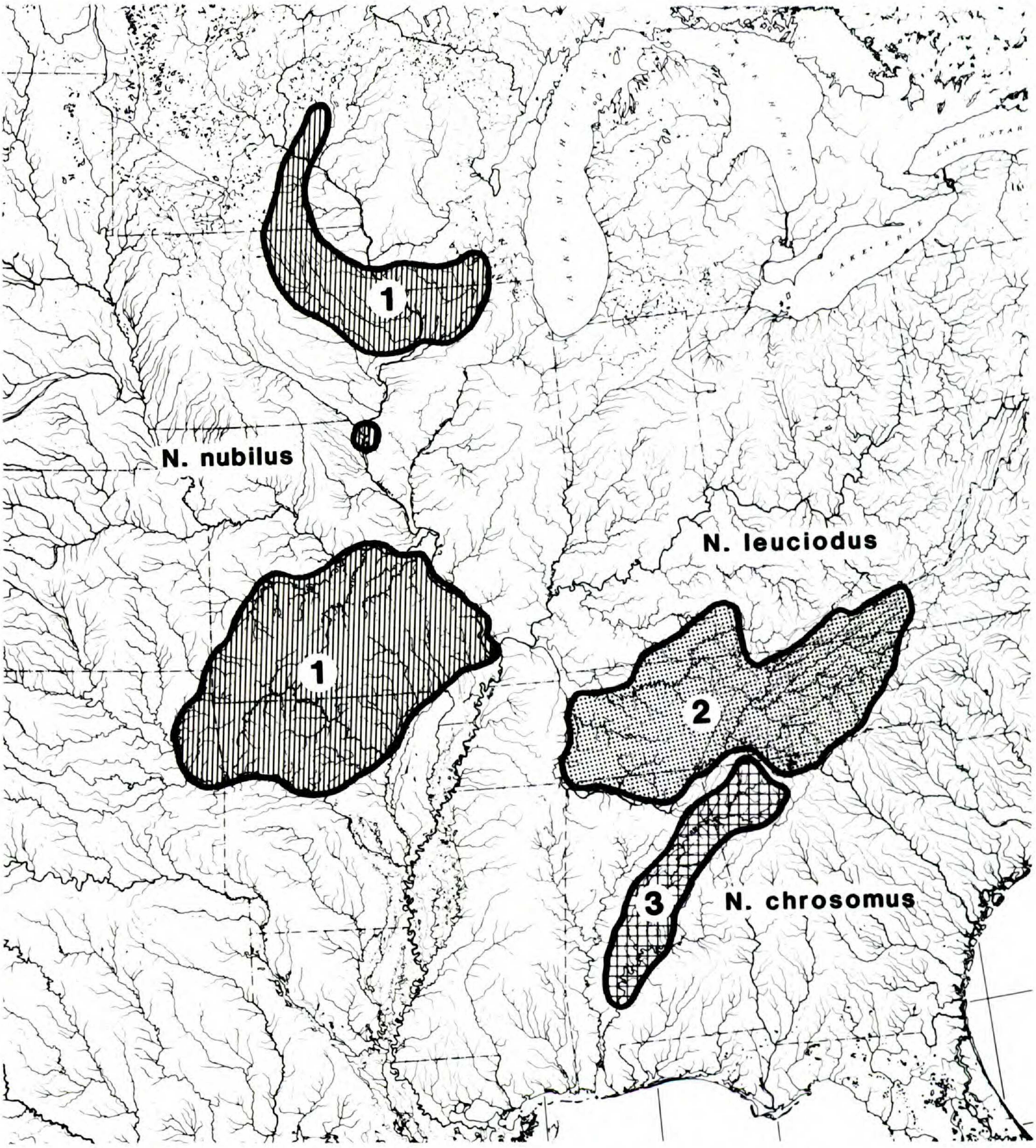

FIGURE 37. Distribution of the *Notropis nubilus* species group (from Lee et al., 1980). Tree: 3+(1+2). Characters supporting monophyly of the group: (1) iridescent breeding colors, (2) dorsolateral pigment pattern on the scales heavily scalloped. Character supporting (1+2): presence of a dashed iridescent predorsal stripe. (Characters from Mayden, unpubl. data.)

the two species does not preclude the hypothesis that *F. waccamensis* is a peripheral isolate derived from *F. diaphanus.*

The problem is that such evidence is relatively weak considering the supposed importance of the phenomenon. In many cases the tentative nature of such speculations are compounded by the fact that the species pair involved is a singular and unique example. In the next section we will suggest that hypotheses of peripheral isolation may be strengthened if we can find additional examples under certain circumstances either in the same clade, or in different clades inhabiting the same region.

Peripheral isolation—multiple speciation events. Single and unique speciation events are

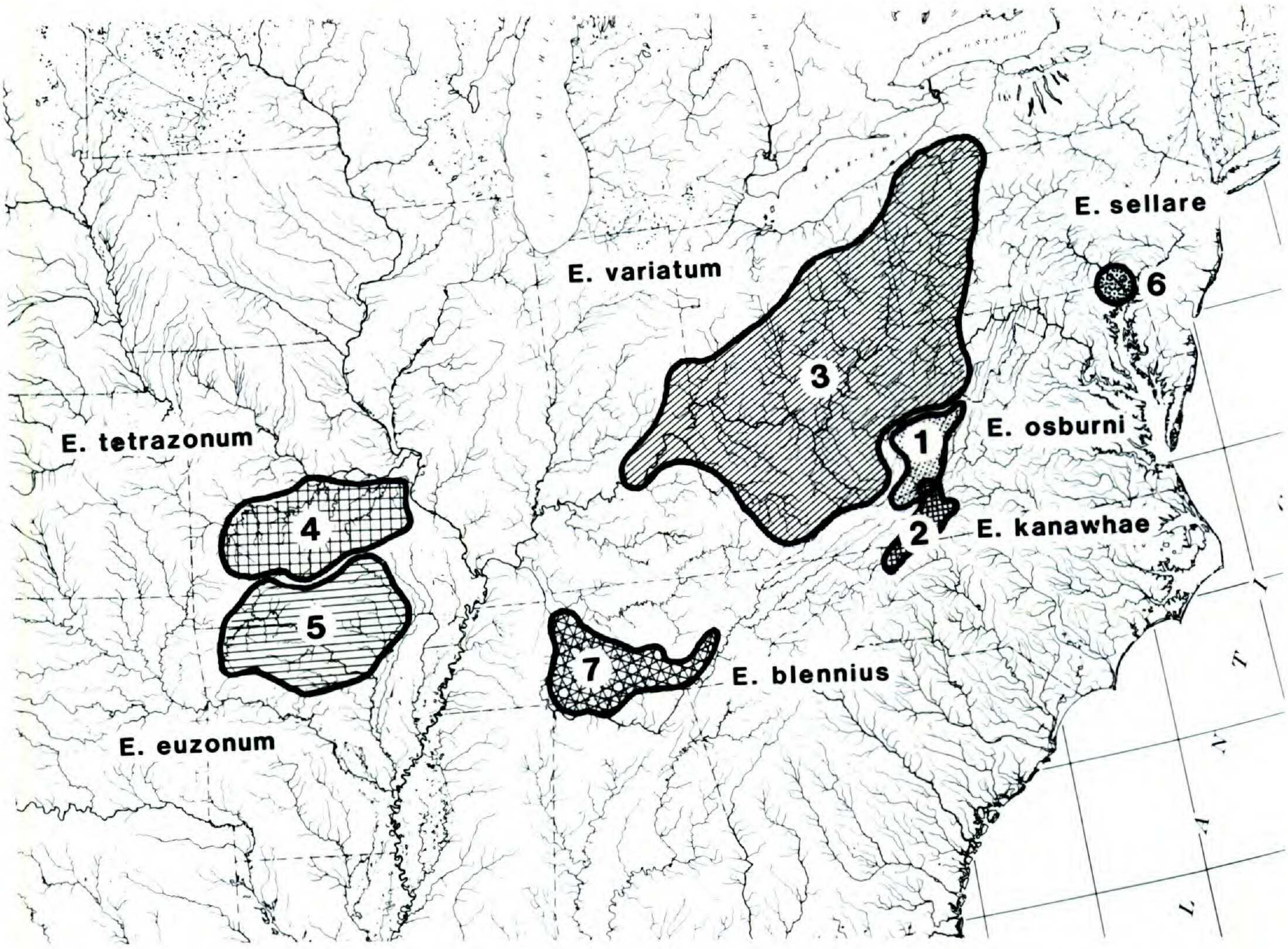

FIGURE 38. Distribution of the *Etheostoma variatum* species group (from Page, 1983). Tree: 7+[[6]+[(3+(1+2))+(4+5)]]. Characters supporting monophyly of the group: (1) fifth infraorbital pore and canal directed dorsally, and (2) large dark dorsal saddles on the body. Characters uniting 1 to 6: (1) anal rays 9, (2) prevomerine teeth present. Characters uniting 1 to 5: (1) breeding tubercles in males and females, (2) brilliant breeding colors. Character uniting (4+5): derived mobility of GPI-2 (100). Character uniting 1 to 3: vertical bars on caudal peduncle continuous ventrally. Characters uniting (1+2): (1) 10 vertical bars on side of body, (2) yellow-gold bar on face. (Characters from Mayden, unpubl. data.)

not easy systems to work with because we lack degrees of freedom to speculate about the possible effects of dispersal, selection, and other phenomena that could lead us to the wrong hypothesis. A clade containing several species, more than one of which had some characteristics of peripheral isolates, or a biota containing an area of endemism inhabited by several suspected peripheral isolates would give us more room to speculate.

Wiley (1981) considered patterns of descent involving peripheral isolation. One case involves an ancestor that "buds off" more than one descendant. Since the two descendants do not share a unique history, they have nothing in common other than sharing an ancestor (i.e., they lack synapomorphies uniting them). If the ancestor remained conservative and if it were treated as a single unit, a trichotomy would be obtained. If the peripheral isolation events were far enough separated in time and the ancestor was evolving, a dichotomy would be obtained. If the ancestor was very widespread and geographically variable, and there were numerous peripheral isolates, a cladistic analysis might show a very complex phylogeny with the population samples of the ancestor appearing on the phylogeny next to or close to peripheral isolates in geographic proximity. We have no such examples in fishes, but if Shaffer's (1984) cladistic analysis of Mexican ambystomatid salamanders is fairly accurate, the phylogenetic pattern he obtained is what we would expect to see. Populations of *Ambystoma tigrinum* (the suspected ancestor, widespread in North America and found in each of the endemic basins of the Mesa Central) appears in the phylogeny interdigitated among no less than 12 species (including both terrestrial and aquatic forms), of very limited range.

The second approach is to search for different

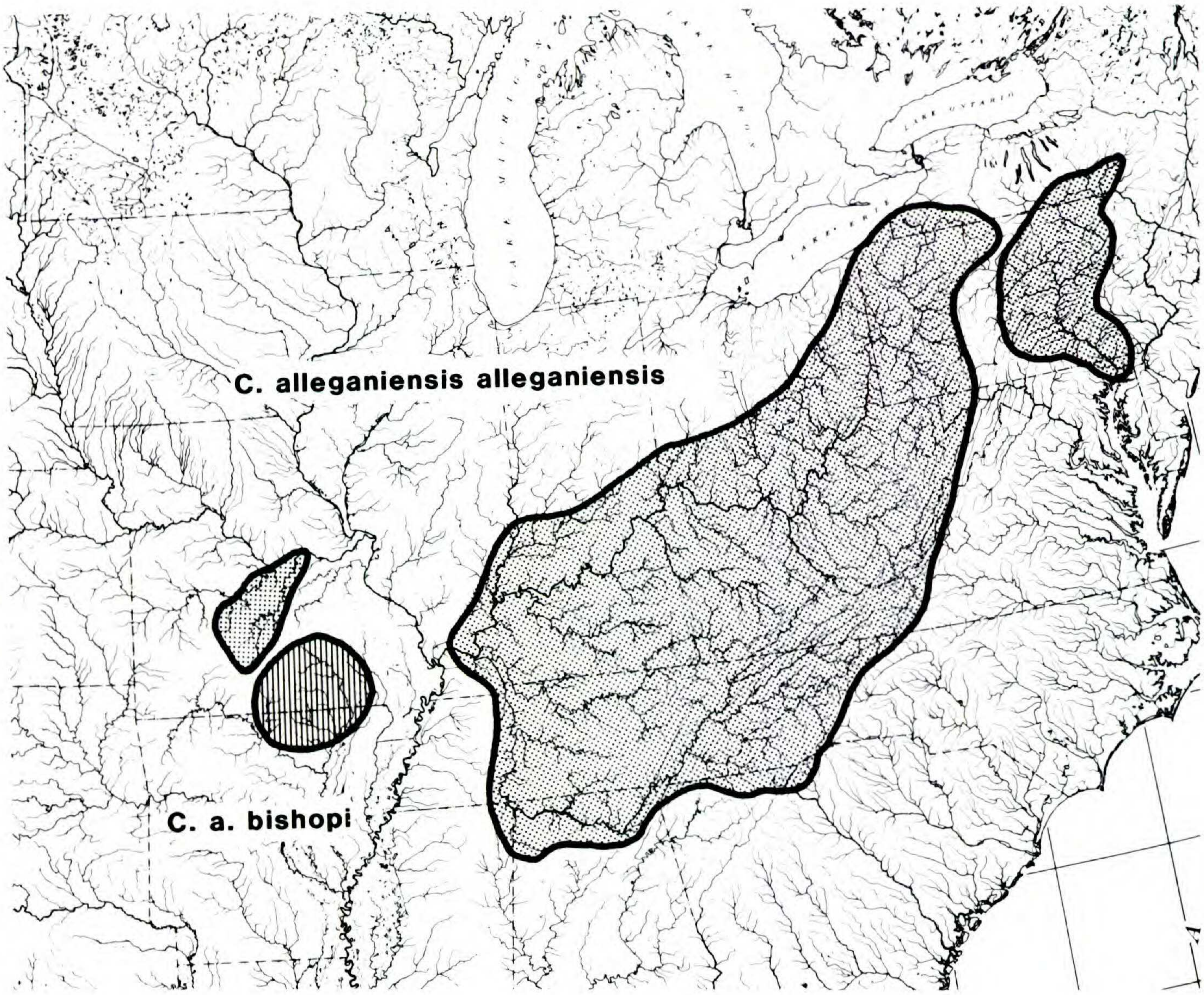

FIGURE 39. Distribution of *Cryptobranchus alleganiensis* (from Conant, 1975).

groups that have endemics in the same restricted area. We can then use the methods of vicariance biogeography to examine the phylogenetic and biogeographic relationships of the endemics to their sister species. For example, Lake Waccamaw has three endemic species of fishes, each with a widespread sister species. One is *F. waccamensis.* The second is *Menidia extensa* (a silverside). It is related to the wide-ranging coastal species *M. beryllina.* The third is *Etheostoma perlongum,* a darter related to *E. omstedi.* The distributions of the three species pairs are shown in Figure 43. Note that the three widespread species have little in common, their ranges do not coincide, they have different ecologies, and they are very distantly related. Given these observations, coupled with the relatively late origin of Lake Waccamaw, it is improbable that the scenarios in Figure 42c, d, and e can explain a distributional pattern in which there is geographic congruence of three unrelated endemics but little congruence between the closest relatives of these endemics other than the fact that each is found around the lake. The best explanation seems to be Figure 42b. Finally, we note that Lake Waccamaw has a diverse fish fauna (Hubbs & Raney, 1946), and the vast majority of species have not speciated in the lake. This indicates that while unique ecological circumstances might promote differentiation; differentiation is not an automatic consequence of changing the ecological parameters a population finds itself in.

The North American fish fauna contains many species whose distributions suggest peripheral isolation, especially among darters and minnows. For example, *Notropis procne* is a widespread species while its sister species, *N. mekistocholas* (Snelson, 1971) has a limited and peripheral distribution (Fig. 44). We might entertain the hypothesis that the origin of *N. mekistocholas* involved peripheral isolation and that *N. procne* is the extant ancestor. However, our

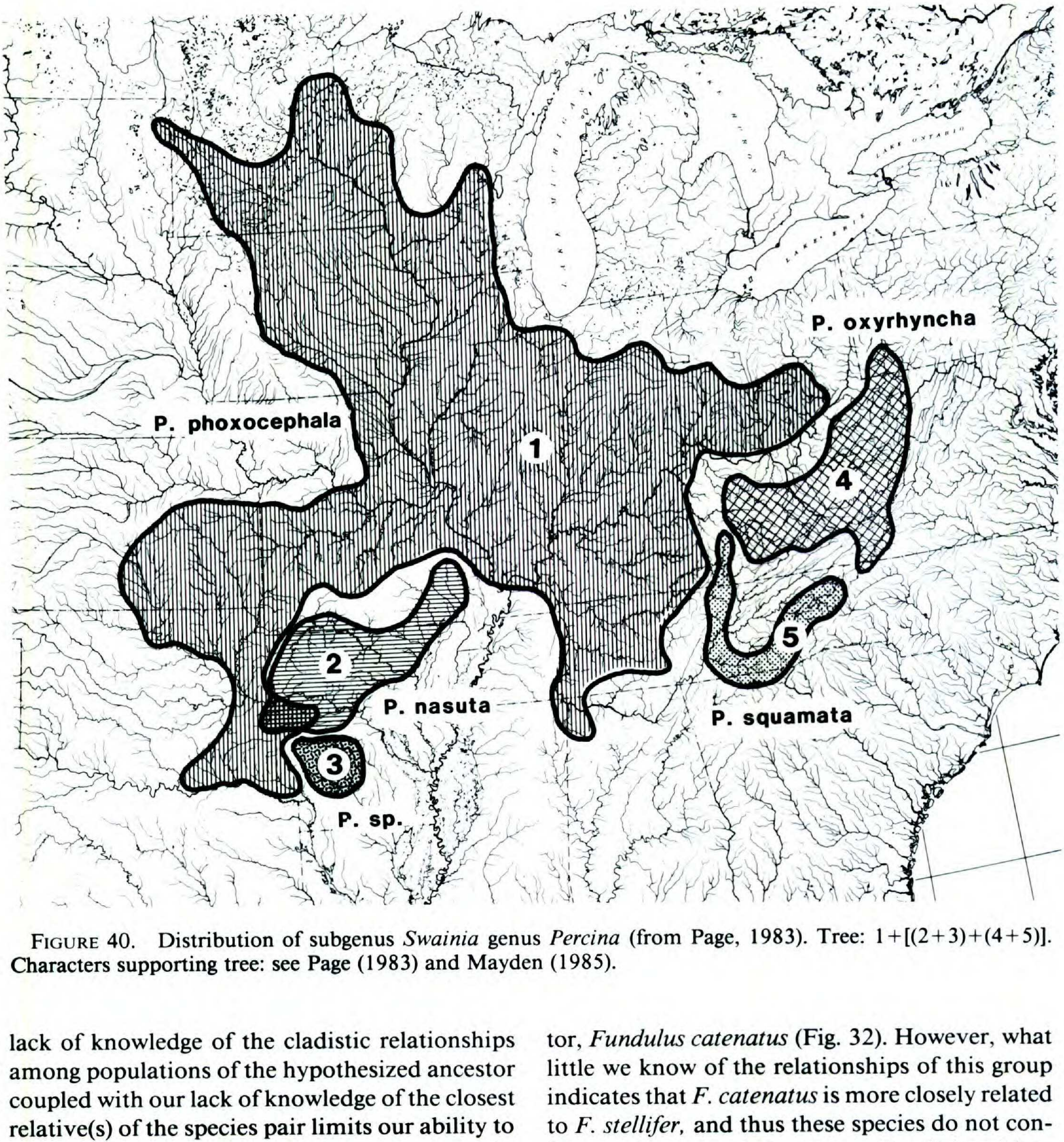

FIGURE 40. Distribution of subgenus *Swainia* genus *Percina* (from Page, 1983). Tree: 1+[(2+3)+(4+5)]. Characters supporting tree: see Page (1983) and Mayden (1985).

lack of knowledge of the cladistic relationships among populations of the hypothesized ancestor coupled with our lack of knowledge of the closest relative(s) of the species pair limits our ability to follow up our analysis. We can neither test the proposition by showing that some population or populations of *N. procne* are cladistically nearer the descendant for some characters nor can we show that the putative descendant conforms to the deviation rule of Hennig (1966).

Perhaps as important as finding criteria from which one can use phylogenetic analysis to corroborate hypotheses of peripheral isolation is to find cases in which phylogenetic analysis causes rejection of the hypothesis or indicates a need for collection of additional data. For example, *Fundulus albolineatus* and *F. julisia* are two obvious candidates for the peripheral isolates hypothesis and are surrounded by a possible ancestor, *Fundulus catenatus* (Fig. 32). However, what little we know of the relationships of this group indicates that *F. catenatus* is more closely related to *F. stellifer,* and thus these species do not conform to the expected pattern of peripheral isolates and their ancestors (Wiley, in press; data from Williams & Etnier, 1982).

The continuum of allopatric speciation from large-scale vicariance and peripheral isolation is apparent when we consider "mini-vicariance." Mayden (1985) has examined several species found in the Ouachita Highlands whose closest relatives inhabit the surrounding lowlands. These include eight species of fishes: two minnows (*Notropis perpallidus* and an undescribed species), two madtom catfishes (*Noturus lachneri* and *N. taylori*), four darters (*Etheostoma pallididorsum, E. radiosum, Percina pantherina,* and an undescribed species). In addition there are six species

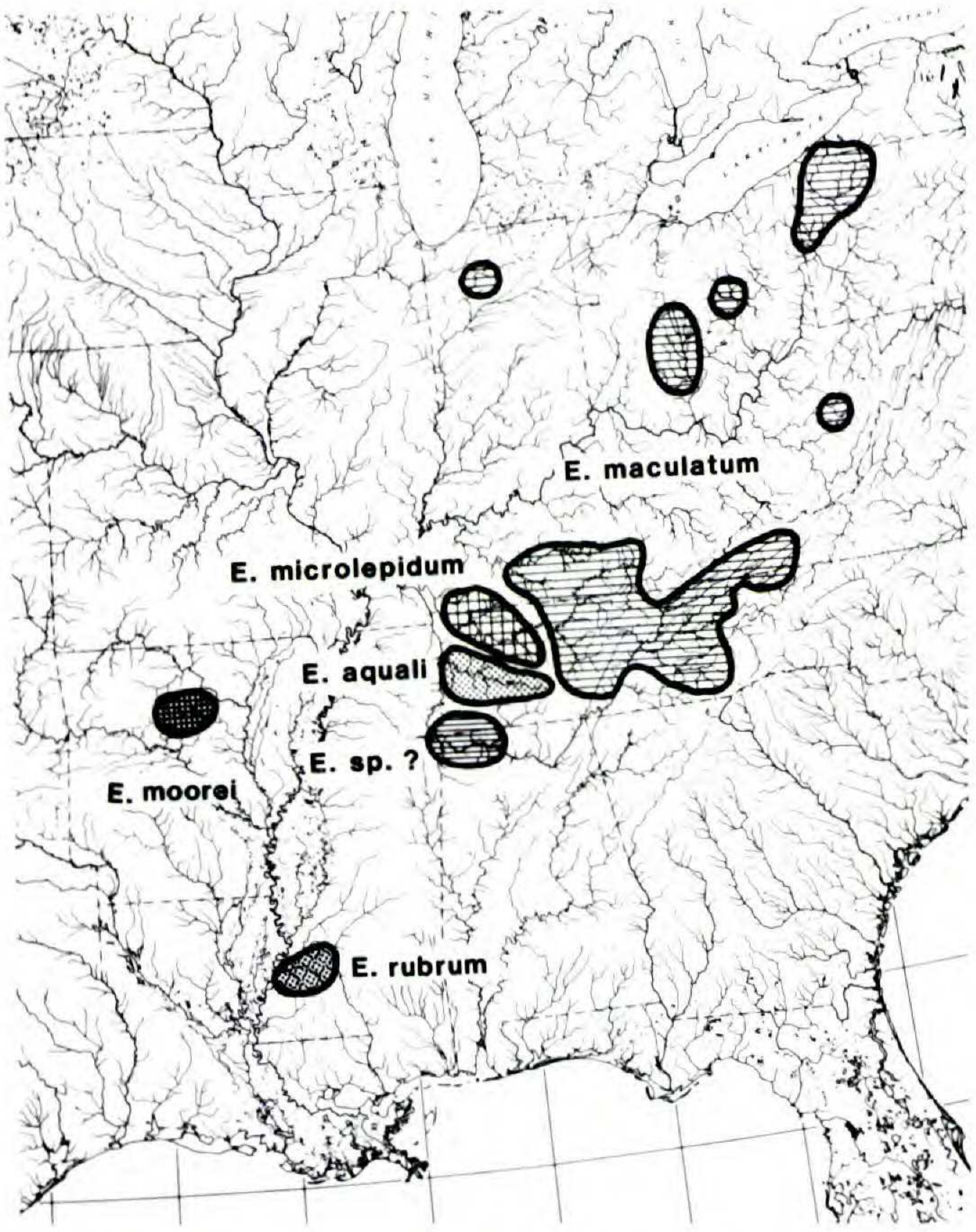

FIGURE 41. Distribution of the *Etheostoma maculatum* species group (from Williams & Etnier, 1982 and Page, 1983). Tree: relationships unresolved.

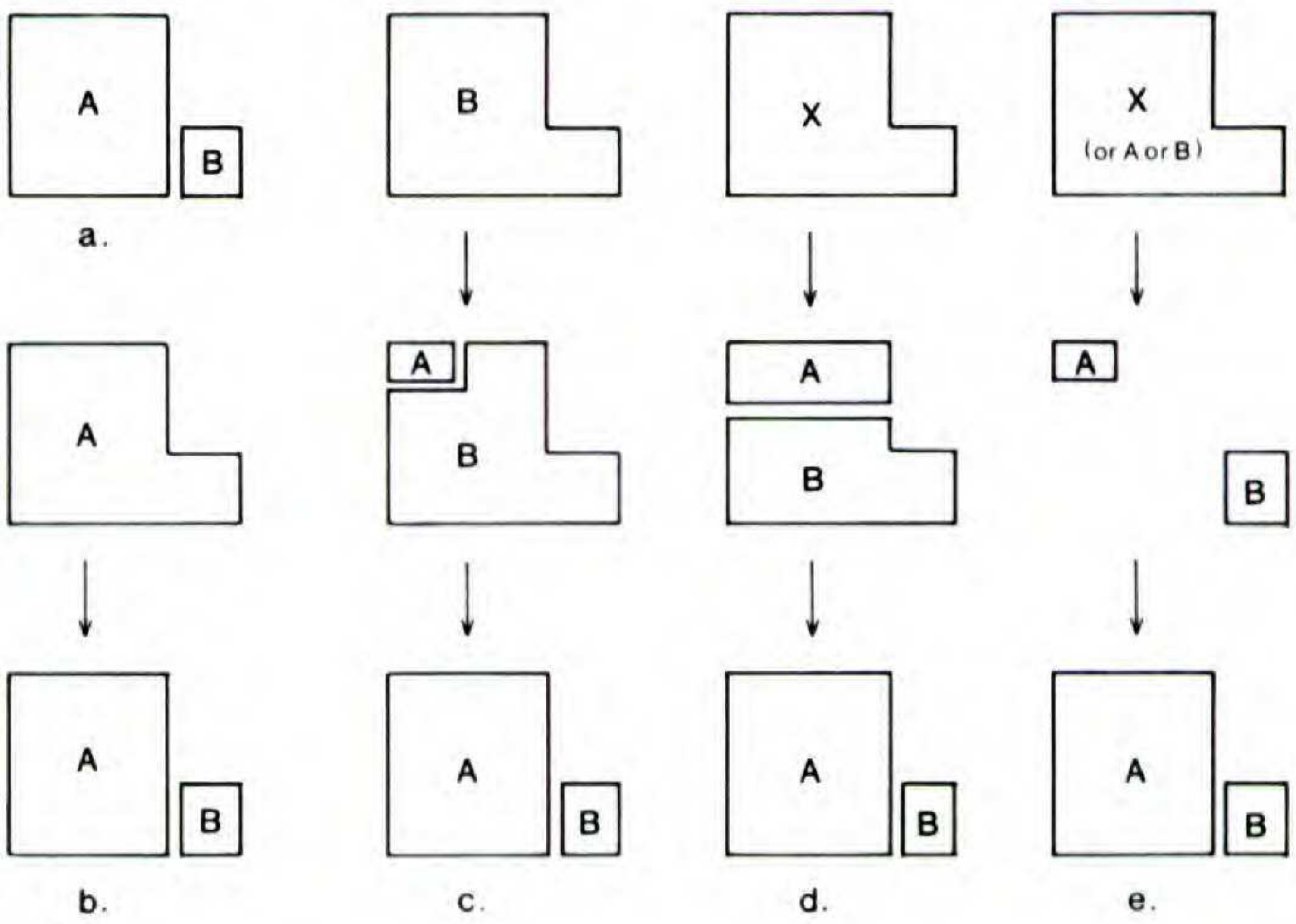

FIGURE 42. Scenarios concerning the evolution of species A and B.

of crayfishes: *Orconectes leptogonopodus, O. menae, Procambarus ouachitae, P. parasimulans, P. reimeri,* and *P. tenuis* (for references see Mayden, 1985). The congruence observed points to a common vicariance event involving the Ozark Highlands, possibly associated with the dissection of the Interior Highlands by the Arkansas River, and a common event with species surrounding or south of the highlands. The fact that a relatively small geographic region was involved makes this pattern a candidate for "vicariant peripheral isolation."

There are many North American fishes that have restricted distributions, making them candidates for the peripheral isolation model. While some can be dismissed because of age or obvious extinction patterns, others cannot be so lightly dismissed. Our major problem, however, is that we lack the phylogenetic information needed to do the necessary kinds of analyses to test the model.

ALLO-PARAPATRIC AND PARAPATRIC SPECIATION

Allo-parapatric speciation occurs when two populations of an ancestral species become disjunct, differentiate to some degree during the time they are allopatric, become sympatric in a limited area, and complete their divergence because of interactions in the zone of sympatry. Parapatric speciation occurs when two populations attain lineage independance while maintaining a narrow zone of contact (see Wiley, 1981, for summaries of both models). Both models are hard to test, at least in fishes. An investigator postulating the allo-parapatric model must demonstrate that (1) the contact zone is a secondary zone achieved after a disjunction, and (2) that the differences observed between the species have either been evolved or "perfected" because of the interactions within the contact zone. An investigator postulating the parapatric model must demonstrate that (1) the contact zone is a primary zone, and (2) the differences we observe have been achieved in spite of the contact between the two species. The simple observation of the presence of the contact zone is not sufficient. Testability is confounded because except for the presence of the contact zone itself, the phylogenetic and biogeographic predictions we can derive from both models are similar to those we can derive from the various modes of allopatric speciation (Wiley, 1981).

We do not have examples of either of these modes of speciation in the North American fish fauna. There are several reasons for this. First, it has been a tradition among North American ichthyologists to favor a rather strict definition of the biological species concept. Thus nominal taxa showing even limited interbreeding within a contact zone are usually considered as a single species and the possibility of either mode operating is never considered. Second, freshwater fishes are confined to the streams they inhabit

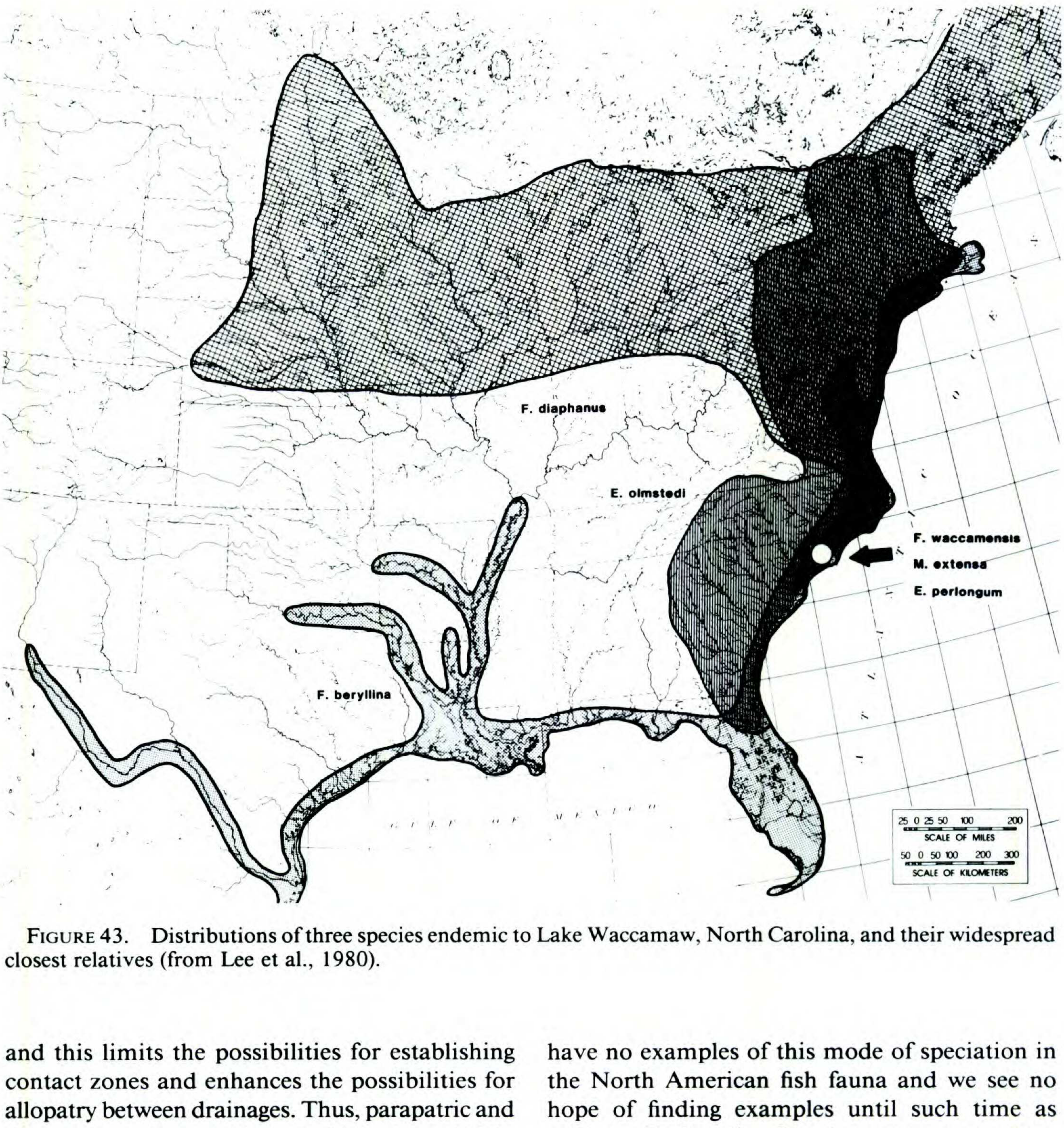

FIGURE 43. Distributions of three species endemic to Lake Waccamaw, North Carolina, and their widespread closest relatives (from Lee et al., 1980).

and this limits the possibilities for establishing contact zones and enhances the possibilities for allopatry between drainages. Thus, parapatric and allo-parapatric speciation would be expected to be largely confined to within-drainage systems situations. Third, we of the ichthyological community simply have not been looking for evidence of either mode because we tend to think "allopatrically."

STASIPATRIC SPECIATION

Although stasipatric speciation has frequently been considered synonymous with parapatric speciation, we restrict it to a mode of speciation involving chromosome mutations coupled with some mechanism such as drift or meiotic drive to fix the mutation in a small population, following the model presented by White (1978). We have no examples of this mode of speciation in the North American fish fauna and we see no hope of finding examples until such time as methods for banding fish chromosomes are generally made available.

SYMPATRIC SPECIATION

As discussed by Wiley (1981), there are several modes of speciation that do not depend on any degree of geographic subdivision and thus can be termed "sympatric" modes. There are no examples of North American fishes that show an ecological mode of sympatric speciation. There are examples involving hybridization and sexual shifts that have produced unisexual species. These include two well-documented examples.

Poecilia formosa is a gynogenetic species (Hubbs, 1964) found in northern Mexico and

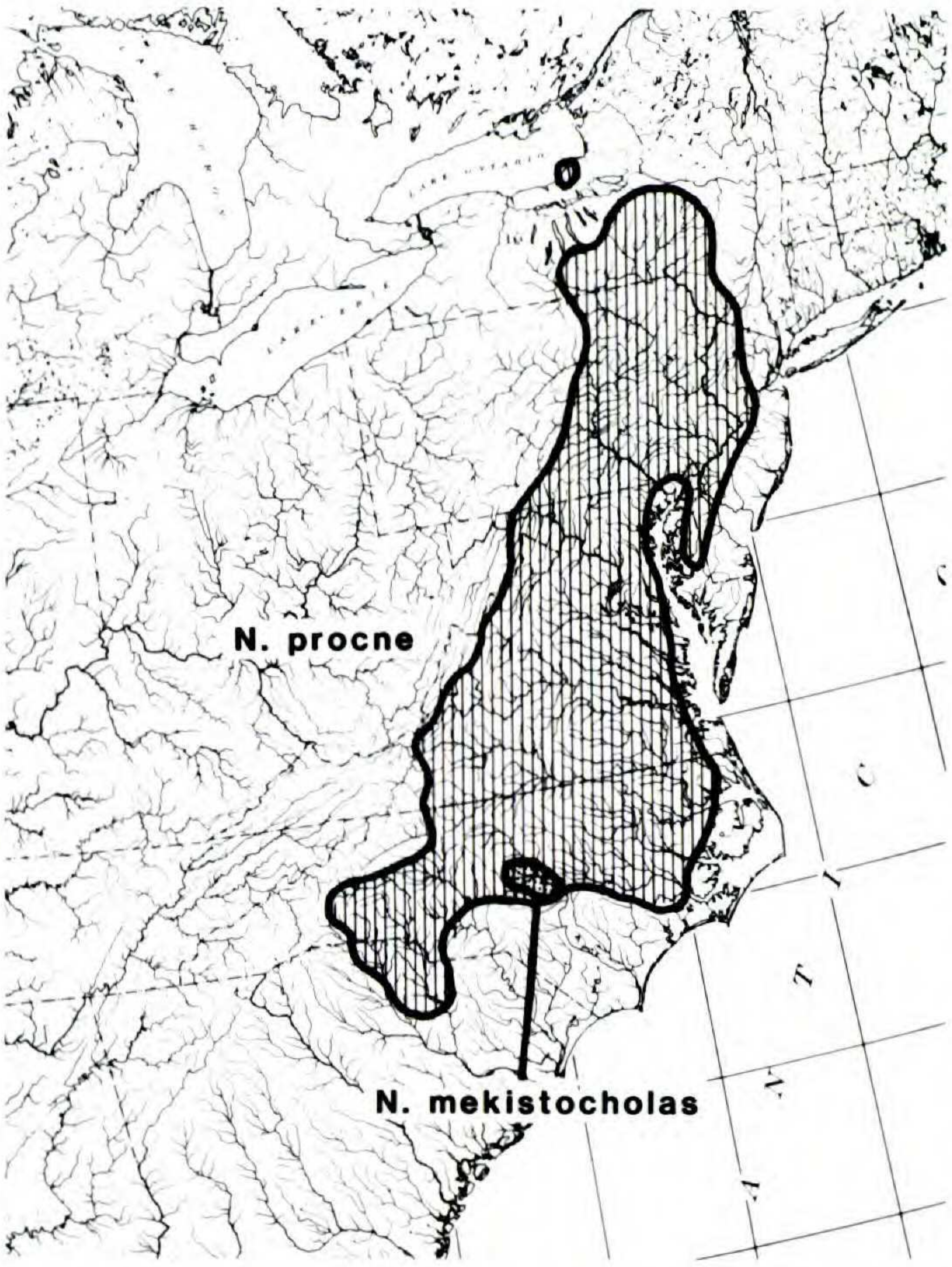

FIGURE 44. Distribution of *Notropis procne* and *N. mekistocholas* (from Lee et al., 1980).

southern Texas. Hubbs and Hubbs (1932) suggested that this species originated by hybridization between the bisexual species *P. latipinna* and *P. sphenops.* [Species composition of the *P. sphenops* complex is not clear (Schultz & Miller, 1971) and the species involved in the hybridization event could have been *P. mexicana* or *P. sphenops*.] Although *P. latipinna* and members of the *P. sphenops* complex are in the same subgenus, they are not considered very close relatives.

Menidia clarkhubbsi is a unisexual species of silverside found at three different locations in Texas (Echelle & Mosier, 1982). Echelle and Mosier (1982) hypothesized that the species arose via hybridization between two species, *M. beryllina* and *M. peninsulae.* The parental species are not sister species. *Menidia beryllina* is more closely related to *M. extensa* than to *M. peninsulae* (Johnson, 1975).

In addition, there are at least five "forms" of the topminnow genus *Poeciliopsis* that are composed of parthenogenic females (Schultz, 1967; Moore et al., 1970). However, the nomenclature and relationships of these forms are not clear (R. R. Miller, pers. comm.). They may be examples of species derived from hybridization and sexual shifts, sexual shifts alone, or morphs within their respective species.

DISCUSSION AND CONCLUSIONS

Analysis of phylogenetic and biogeographic patterns of descent and attempts to correlate these patterns with modes of speciation has hardly begun. Our attempts with selected North American fishes is a preliminary effort, but they suggest that such correlations can be made. Our first example, the Northern Gulf Coast, suggests a pattern of large-scale allopatry (model I) involving several clades. We note that the number of species involved is small relative to the number of species inhabiting the region and that the groups themselves do not comprise a "biota" in the sense discussed by vicariance biogeographers (Fig. 45). Further, not all speciation followed a common pattern. Our second example, the Central Highlands, can only be considered a counter example. We observe vicariance without consequent speciation. Apparently the species inhabiting the regions were present before the vicariance event that caused the disjunction of the fauna. However, the effects of vicariance can be seen within the Interior Highlands in a pattern of "mini-vicariance" in the Ouachita Highlands.

Our attempt to corroborate the peripheral isolation hypothesis proposed by previous workers for three species endemic to Lake Waccamaw met with success, but although other biogeographic patterns involving putative ancestors and descendants are suggestive of this phenomenon, we lack the phylogenetic and biogeographic information necessary to pursue such hypotheses. Two examples of multiple peripheral isolation were examined. In one (*Fundulus catenatus, F. julisia,* and *F. albolineatus*) hypotheses that the two species of restricted distribution are peripheral isolates of the wide-ranging species are not corroborated because the wide-ranging species, *F. catenatus,* is more closely related to *F. stellifer.* This does not falsify either hypothesis, but it does require that we must minimally entertain the idea that *F. catenatus* has evolved anagenetically and given rise to *F. stellifer* after the origin of the two peripheral isolates if it is, indeed the ancestor. (But if this is true, would the species that gave rise to *F. albolineatus* and *F. julisia* be *F. catenatus*?) The other example, species of ambystomatid salamanders of the Mesa Central seems to offer a clearer picture, but we need examples among fishes.

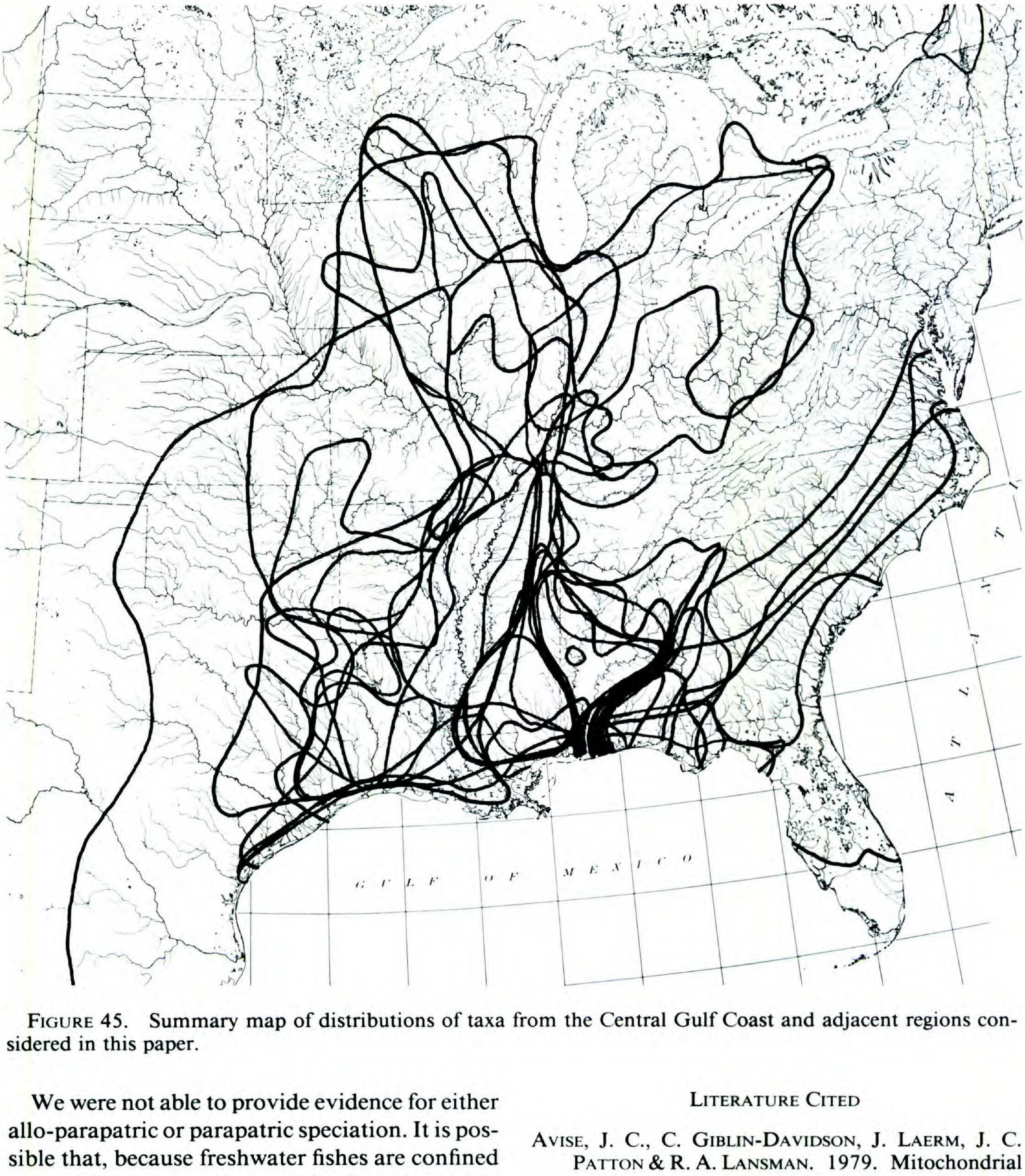

FIGURE 45. Summary map of distributions of taxa from the Central Gulf Coast and adjacent regions considered in this paper.

We were not able to provide evidence for either allo-parapatric or parapatric speciation. It is possible that, because freshwater fishes are confined to their streams, the opportunity for either mode to operate is restricted. Perhaps studies of coastal species where this restriction is not present will provide an opportunity to demonstrate these modes of speciation.

The only sympatric mode of speciation well documented in the North American fish fauna is speciation via hybridization associated with asexual or gynogenetic reproduction of all-female descendants. In neither case were the species of hybrid origin the result of hybridization between closest relatives.

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